LESLIE REID

The Sociology of Nature

WITH TWELVE PLATES AND
EIGHT FIGURES

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TO MY WIFE

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FOREWORD

In this book an attempt has been made to describe the beauty and complexity of the life of animals in relation to their environment which is the surface of this earth and the conditions of climate, soil and plant-life which govern it. The book cannot fail to be concerned also, and continuously, with the relationship of animals to one another, this means that the greater part of it is an exposition of facts, a setting forth of recognized phenomena; but that cannot be quite all. Facts are of the greatest interest in themselves but can have little real value apart from their significance as the raw materials of something more. Recorded observations require to be explained, and the explanations in their turn require to be used as bricks with which to set up some sort of edifice of interpretation. To say that this is an ambitious undertaking is to make an understatement. Nevertheless it is an undertaking that men have been engaged upon since first they became capable of disinterested thought. In doing so they have adopted two distinct and in many ways conflicting methods, the method of religion grounded upon faith, and the method of science grounded upon reason. My concern is with the second of these, but that exercise of reason involves also an act of faith and a fundamentally important one, faith that is to say in reason, in the ability of reason to bring us ultimately to the truth. So the two methods, to that extent at least, are in harmony.

The student of the natural world, applying himself in this spirit of reason, grounded on faith in the efficacy of reason, cannot fail to be impressed by the width and the depth of the knowledge that science has already amassed. There is no doubt that we know much, but this respect for the power of human reasoning brings with it another profound realization, that of the immensity of the field remaining to be explored. It is a commonplace that the more we know the more deeply do we become aware of our ignorance. Each winning to the known opens up a fresh vista of the unknown. The result is, or should be, scientific humility, and it is on this score that scientists have been most frequently attacked, for their lack of humility, for their tendency

to dogmatize. With this in mind and in no spirit of dogma, I venture to declare another act of faith.

Broadly speaking there are two opposed points of view with regard to the world of nature. The first looks upon that world as the product of blind forces, devoid of a recognizable plan, undirected by any approximation to what we call a mind, organized on the basis of chance. The second cannot agree that the forces are blind, is aware however uncertainly of a plan and therefore of a directing mind, is revolted by the thought of a universe governed only by the law that governs the tossing of a coin. To a large extent this is an example of the conflict between reason and faith, those adhering to the first view producing evidence in support of their conclusion, while at the same time declaring that evidence is the one thing their critics cannot produce. There is some truth in this, but it is far from comprising the whole truth; and it is one of the purposes of this book to show that evidence in favour of a planned world is unmistakable. It is to be seen in the first place in the unity that binds the manifestations of nature into an integrated whole, each one of these manifestations depending on the others with an intimacy that besides being vitally necessary is also frequently mutual. This is set out in the first chapter. Subsequent chapters enlarge upon the theme, pointing out that the principle of dependence governs the lives of all creatures, that even the struggle for existence is an organized struggle, and that in addition to keen and sometimes bitter competition, there is also cooperation between animals and plants, between one species of animal and another, and finally between animals of the same species. It can hardly be denied that this unity on the one hand, and this organization of an exceedingly complex kind on the other, provide evidence of planning, of a directing, creative mind somehow and everywhere at work. Further evidence is presented in the chapter on evolution.

A world governed by chance could not be the organized world that this book attempts to describe. Unity and organization are incompatible with what we call chance. That is a declaration of faith reinforced by reason, but it relies in another sense on reason, for it is my firm conviction that whatever mind has planned this world fulfils the plan by means of what we call natural agencies, those that is to say that we are capable of observing and understanding for ourselves through the exercise of our reasoning

faculty. We are no more than at the beginning of a complete apprehension of the wonder and glory of the natural world, but the end lies within our reach. Our reasoning is fallible, as we are, which means that we frequently stray. Our journey along the road of truth is fumbling and hesitant, but we shall come to the end at last.

L. R.

I

THE ELEMENTS

The common growth of Mother Earth
Suffices me.
WORDSWORTH: *Peter Bell*

PERHAPS the most striking, the most moving, thing about the wild creatures in all their widespread diversity, still teeming over the surface of the earth, is the simple fact that they do so, that in the words of Mallory explaining his desire to climb Mount Everest, they are there. We, or some of us in our egocentric way, are sometimes heard to ask: 'What good are they?' But this is a question unlikely even to occur to anyone who has taken the trouble to examine them and their ways. The student of natural history knows that they exist in their own right, and that this is an important part of their fascination. They live their own lives sublimely independent of humanity, except when humanity intervenes to extirpate them because they get in the way of its feverish activities. They were tenants of this planet long before man ceased to be an ape-like creature, many of them by hundreds of millions of years. Their frail yet marvellously enduring generations have succeeded one another over a lapse of time for which the hackneyed adjective immemorial is an absurd understatement.

Think of *Volvox*, that minute, emerald-green plant-animal, rolling now in serene detachment through a drop of water on the slide of a microscope, then of all the hosts of *Volvox* as having rolled in identical serenity for almost as long as life has existed. Think of all the creatures inhabiting a coral reef in kaleidoscopic variety, of beetles in the grass, ants in their thronged cities, butterflies lapping up the moisture of a sand-bank flanking some tropical river, ripple-marked fishes in rippling movement, gannets nesting in their thousands on some unvisited island. All these and uncountably more rely

wholly on themselves and on one another. They exist for us to wonder at.

But after all there is much more to move us than this fact of self-sufficient existence. Their diversity is equally a subject for wonder, as is their irrepressible urge to propagate their kind, their grip upon life, and perhaps above all the way their structure and habits are adapted to the environment in which they live. To wish to understand something of their lives and ways, and to pursue this quest in a disinterested spirit, believing that such knowledge is worth having for its own sake, is an admirable thing. It has resulted in the accumulation of an imposing corpus of theory and conclusion which is among the greatest achievements of human mind, but an achievement almost solely of recent times. At the beginning there was bewilderment, an attempt with many a false start to grasp the significance of the wood without first examining the trees. Before long it became clear that no single intelligence could hope to cover the whole field. For this reason there arose the specialist, whose business it became to isolate circumscribed departments of knowledge and give them his whole attention. His method was analytical, a breaking down, a dividing. This went on in spite of a growing realization that it was the wood as a whole that mattered, that specialization can never be an end in itself. Analysis must give way to synthesis, since the further specialization continues the clearer does it become that a close dependence exists, not only between the different branches of a science, but between one science and another. Science therefore, having given detailed attention to the trees, is now turning its attention to the wood, is coming back in fact to the viewpoint of the earliest inquirers, with the all-important difference that it is now provided with the raw materials for synthesis, the varied contributions of the specialists.

There is little doubt that this is true of science as a whole. It is certainly true of the science of biology, in which perhaps there has been more specialization than in any other. A synthesis is now well under way, and we call it ecology, which can be defined as the study of living things in relation to their

surroundings and to one another. The more deeply ecology is studied, and it is still in its early stages, the clearer does it become that mutual dependence is a governing principle, that animals are bound to one another by unbreakable ties of dependence. But that is no more than a fraction of the truth, for the ties of dependence linking animals with one another are no closer than those linking animals with plants, while plants in their turn cannot be dissociated from climate, nor from the earth itself in the form of rocks and soil. Without plants there could be no animals, without soil and without rainfall there could be no plants. Nor are the several ties traceable in one direction only. If animals depend on plants, so in a number of vitally important ways do plants depend on animals. Similarly, while plants cannot exist without soil, neither can soil exist as such without contributions made to it by plants. Yet again, rainfall is a vital necessity for plants, and plants in the form of trees are not without their influence in the making of rain, while playing a part of the greatest importance in helping to conserve the rain for their own use after it has soaked into the soil. If trees can be said to increase rainfall, so to a very much greater extent do mountains. So the earth, which cannot support life without the rain that the plants require, plays its part in adding to the supply.

What has just been written is no more than a bare summary of a fundamental principle governing the existence of life. I shall return to it again and again. There is another fundamental principle that the modern study of ecology brings out, and that is change. It was the Greek philosopher Heraclitus who, as long ago as the sixth century B.C., summed up his teaching in the sentence 'all things flow'. Denying the reality of static existence, he declared that eternal flux was the condition of the universe. With all things in nature, according to him, it is not a matter of being but of becoming, a dynamic process of transition. He declared further that the primordial substance of the universe was fire. Today we know better than to agree with the second of these conclusions, but the ecologist of modern times will certainly agree whole-heartedly with the first.

Both biologists and geologists of today are well aware of the soundness of that doctrine and can offer proof entirely unknown to Heraclitus, who after all was no scientist as we understand the term.

Much of the evidence in favour of Heraclitus' dictum is simple and apparent. We can see it for ourselves, can hardly help seeing it, for indeed it governs our lives. The sun rises and sets as the earth rotates. The seasons succeed one another as the earth speeds on its orbit round the sun, its axis making a never-changing angle with the plane of that orbit. The seed germinates, the seedling proliferates into leaves, flowers, and fruit. Every animal, from the most primitive up to man himself, undergoes a life-cycle which is one continuous change. These and a hundred others like them are appreciable to us because the phase of their fulfilment falls well within the span of human life. They are the short-term, obvious changes, and the very first men of all were certainly aware of them. They have the utmost relevance for ecology. But there are others, equally relevant, but far less easily perceptible because slower, more gradual, some requiring a span equivalent to many human lives, others of such gradualness that we are quite incapable of seeing them directly and can infer their existence only from the traces they have left. Such are the slow, secular changes of climate, the onset and recession of glaciers, the transgression and withdrawal of seas, the deposition of sediments to form rocks, the erosion of mountains. It is only within the past 150 years that we have become aware of fluxations of that order. Their realization was one of the major revolutions in human thought; and intimately linked with them was the realization of changing, developing life, the doctrine of evolution, which indeed was one of them, perhaps the most important.

We see further that it is not merely the notion of change that matters, but the inevitable gradualness of change. In nature there are few abrupt transitions, for on the whole she abhors them. This applies even to the transitions in space that we can see for ourselves. Abrupt enough to a casual glance, they are

seen to be less so when looked at more closely. That between sea and land for instance is traceable, not as a line but as a zone, that between tidemarks, which in truth is a zone involving both space and time. Apart from this, the things of the land – birds, plants, insects – invade to some extent the kingdom of the sea; while the influence of the sea penetrates landwards to a notable and varying extent. In a similar way the snow-line on mountains ebbs and flows with the seasons, forests grade into savanna or steppe, savanna and steppe into desert. Broadly speaking we can say that it is only when the normal gradualness of a change has in some way and for some time been prevented that it takes place suddenly and with violence.

This conception of the gradualness of change is bound up with certain primary, and to us sharply defined distinctions. We make one of this sort for instance between the two kinds of life, plant and animal; and while there is no denying that the distinction is a valid one, it has long been recognized that there are many unicellular organisms having the attributes of both. We cannot say that they are exclusively either the one or the other. The change from plant to animal, in origin at least, was a gradual one. Another and even more sharply defined distinction, to us the most important of all, is that between the living and the non-living. We are convinced that every particle of matter in the universe is either the one or the other. But even that distinction has lost a large measure of its rigidity in recent times. Crystals are known to possess almost all the attributes of living things; while those still mysterious and infinitesimally small organisms, the filter-passing viruses, behave at one time like inanimate crystals, at another like living things, according to whether they are detached from or are part of the hosts on which they prey. This is a comparatively recent discovery, amounting to, or looking as though it might in time amount to, a revolution in thought in itself. It may be that life evolved from non-life as gradually and by as continuous a process as multicellular from unicellular organisms, or birds from reptiles. It is highly probable that the change from the non-living to the living was as gradual as that from plant to

animal. It may even be that death itself, to us the most violent change of all, is less violent than we suppose.

These two distinctions, between the plant-cell and the animal-cell, between the organic and inorganic; and these two primary principles, mutual dependence and gradual change, cannot fail to be implicit in any survey of the whole complex web of life. The distinctions can be taken for granted, with the reservations already made. As for the two principles they will have to be explicit and that continually, since they are far less easily realized, and since both of them determine the very nature, weave the essential fabric, of the web of life.

The four spheres

The main concern of this book is with animal life, but since plants sustain animals, they must play an important part in it as well. Further, since plants depend utterly on soil on the one hand and on climate on the other, these two also must be given a place in this introductory chapter at least. With this in mind and taking the broadest of views, we can distinguish four great entities or spheres: first the lithosphere which is the outer crust of the earth; secondly the hydrosphere, comprising all the salt waters; thirdly the atmosphere; and lastly the biosphere, a word signifying the network of all animated things, both plant and animal. Of these, where all land-surfaces are concerned, the first and the third provide the indispensable substratum for the maintenance of life, both plant and animal, in all its wonderful diversity.

THE LITHOSPHERE. The deeper parts of the earth's crust are made up of igneous rocks, those that is to say that have cooled and solidified from the molten condition. Over much of the surface as well, rocks of this kind are to be found, granite, basalt and the like; but overlying them elsewhere and covering an enormous area of continent and island, are the rocks of sedimentary origin, laid down for the most part in shallow seas and lakes particle by particle. The connexion between the

two is an intimate one, since the sedimentary rocks – sandstones, limestones, clays – were built up originally from the piecemeal destruction of the igneous. They are in a special sense secondary as well as sedimentary; and the slow, subsequent fragmentation of both kinds is brought about by atmospheric weathering. Then comes erosion, the transportation and the final deposition of the particles by the four great agents of erosion, rivers, glaciers, wind, and sea. Of these four, rivers perhaps are the most important, at least in those parts of the earth where rainfall is sufficient for rivers to flow perennially.

Contemplate imaginatively a rock section where beds say of sandstone are exposed in some quarry. Grasp the fact that their presence is accounted for by geographical conditions obtaining at some remote period, a river flowing into a sea, winding perhaps over a swampy delta, that as it meandered and bifurcated over the delta, and still more when it came to the sea and the current slackened to immobility, a slow rain of particles fell and very gradually accumulated. Realize that those beds of sandstone are the direct result of those conditions, and finally that they represent a period of time during which the conditions held good and that work was done.

In time the conditions are bound to change. The sea at that particular point may deepen, alternatively it may ebb away. If it deepens, perhaps in response to some warping of the crust, the river continues to deposit its particles, but the shallows at the mouth of the river are now at a distance, and the particles continuing to be deposited in the deepening sea are finer because conveyed further offshore. It is only the finer particles that can be so conveyed. For this reason, if the particles are very fine and the sea comparatively deep, the rock being formed will be of a different kind, a clay rather than a sandstone. Here is change and gradual change, as perhaps may be shown in the rock-section exposed in the quarry from the way in which the coarse-textured sandstone shades off into a fine-textured clay. Broadly speaking the finer the particles the deeper the sea and the greater the distance from the landmass

across which the river flowed. This conveys a relationship in space between the two. A relationship in time is simultaneously shown by the fact that the fine-textured clay overlies the coarse-textured sandstone. The first was laid down at a later date than the second.

If the sea on the other hand is slowly ebbing and becoming less deep, the shoreline advances, a widening belt is won from the sea and a fresh land surface will be laid bare, with all that that means in the way of an increasing mantle of living things. In that event no sedimentation can occur. Picture a change of yet another kind. The river may be diverted or dry up altogether because of some alteration of climate. The sea is then clear of sediment, and there may occur a slow precipitation of of lime steadily accumulating over the floor. This, together with the mingling deposition of the shells of dead creatures, or of countless millions of the tests of minute organisms, will give rise to beds of limestone, or of chalk which is a form of limestone.

Changes of this sort, slow, rhythmic pulsations, responding to warpings and heavings of the underlying substratum, or others of a more violent sort, such as oozings of lava from fissures in the crust, explosive eruptions also from time to time, scattering rock fragments and clouds of comminuted dust, have all gone on at intervals succeeding one another, repeating themselves over and over again since the earth cooled from a molten condition some thousands of millions of years ago. In this way there has evolved the crust of the earth as we know it, the lithosphere, layer upon layer, each sooner or later to be exposed, and when exposed acted upon instantly by the agents of erosion and destroyed, so that fresh layers can be laid down elsewhere. The major sorts of rock are comparatively few: granites, basalts, conglomerates, sandstones, limestones, clays, and shales. These, with local variations differing in some sort chemically and in another sort organically, as shown by the fossils they contain, have come into existence over and over again in endless repetition throughout the long history of the earth. They constitute the crust and are

of primary importance for living things, since from them has been formed the soil, the platform for plants and so for animals, that soil which varies from place to place largely according to the size of the particles originally laid down, that size of the particles determining the capacity of the soil to retain the moisture on which the plants depend for their sustenance.

THE ATMOSPHERE. Moisture calls to mind climate, and so to the second great sphere, the atmosphere. Temperature, pressure, rainfall are the things that matter most where climate is concerned. Temperature, varying in the widest sense of all with latitude, is affected also by the angle that the sun makes with the horizon, that is to say according to the seasons, by the distance of any one part of the earth from the sea, by altitude above sea-level. Warm air thins away, cold air is compressed. Thus it is variations in temperature that cause variations in atmospheric pressure measured by the barometer. Variations in pressure cause winds to blow in an attempt to equalize the pressure. Winds bring rain. All the airs that blow hold water-vapour to an extent that varies with the temperature of the air. But there is a limit to the holding capacity, and the point of saturation depends also upon temperature. Reduce the temperature of the saturated air and the water-vapour condenses as rain. The rain-making agency, one of the fundamentally important power-producing engines of the world, is that which cools air. Cooling occurs on a stupendous scale over the great oceans when cold, dry air from polar regions mingles in great swirls with warm, moist air from equatorial latitudes. The moist air is driven upwards by the drier air, cools as it rises and lets fall torrents of rain. These ascending spirals are the depressions we hear about so frequently, and when they reach our continental coasts they are the more likely to bring rain because of the friction of land against air. On a local scale mountains cause further ascent and so further precipitation. Similarly, on a yet more local scale, will forests with the friction they can provide. Apart from this, a tree, and still

more an assemblage of trees, discharges moisture previously sucked from the soil. This is known as transpiration, and it adds inevitably to the humidity of the air, increasing its burden of water-vapour, increasing the likelihood of condensation. So trees, themselves vitally dependent on rainfall, play their part in bringing it about. This is a good example of those intimate, mutual associations of which there are so many in the natural world. Break the association, as man has done in many parts of the world, and the result can be catastrophic where life is concerned, including human life. Cut down trees and you help to make a desert.

THE HYDROSPHERE. So two of the great spheres, the lithosphere and the atmosphere, the one pertaining to the earth, the other ultimately to the sun, in their mutual association provide the conditions needed for the maintenance of life on land, whether plant or animal. But there is a third, the hydrosphere, the great oceans, covering more than seventy per cent of the earth's surface, with the continents after all no more than islands in their midst. Quite apart from this claim to our consideration 'the great salt deep' teems with living things to an extent surpassing dry land, since the world of the waters is a three-dimensional world in a way that the land, even including the air above it, can never be. Since there are animals uncountable in the great waters, there must also be plants; but the distribution of plants on dry land and in the sea is restricted, though for different reasons; on dry land because parts of it are too dry, in the sea because parts of it, indeed the major part, are too dark. Plants must have sunlight to synthesize their food and that of animals. For this reason the larger fixed plants are found in the sea only to the depth penetrable by sunlight, which means the continental shelves, and the plants are seaweeds exclusively. The deeps of the sea, not the ultimate abysses only, but the great oceanic basins below a depth of a hundred fathoms, are devoid of seaweeds. On the other hand the surface waters everywhere, again to the depth penetrable by sunlight, swarm with floating plants of microscopic size,

the diatoms in their uncountable millions. Seaweeds contribute comparatively little to the food of creatures inhabiting the great waters. Diatoms on the other hand are the basis of all the food that there is.

The sea has another claim on our attention, for there is little doubt that it became both the womb and the nursery of life itself. It was in the primeval oceans of the world that life must have originated, perhaps somewhere in the shallows accessible to what little sunlight could penetrate the dense cloudbanks, from which torrential rain fell ceaselessly for months, even years at a time. Somewhere in that dim natural laboratory protoplasm, the stuff of life, was prepared, kneaded, given co-ordinated shape. We can only guess at the nature of the first living organisms, but it is reasonable to suppose that they stood at that borderline between plant and animal, where even today some organisms are to be found. But perhaps it is more likely that they were strictly neither the one nor the other, organisms of a simpler structure than anything we know today, related remotely to the bacteria and capable, like some of them, of ingesting inorganic substances directly.

At a much later date, in response to augmented sunshine, there took place that great parting of the roads, one by way of simple unicellular organisms, green with the first chlorophyll, to all the plants that have since appeared; the other by way of equally simple organisms, lacking chlorophyll and capable of devouring those that possessed it, to all the animals. It was then, along those two associated but diverging paths, that there began that evolution of living things which has resulted in so wonderful a diversity. The oceans began to swarm, first with invertebrate then with vertebrated creatures, but for a long time the oceans, and no doubt the fresh waters, alone. For millions of years life was confined to the waters, while the continents showed nothing but naked rock, were the playground of wind and rain, of glaciers, volcanoes, and blown desert sand, devoid of life, devoid of true soil.

THE BIOSPHERE. Then at a period comparatively advanced i

the history of the earth, there took place that invasion of the land from the sea, that milestone in history if ever there was one. What creatures they were that, in Silurian* times, undertook this laudable enterprise is far from certain, but it is supposed that they were arthropods, perhaps scorpion-like things. Considering what the consequences were to be we are justified in calling this an invasion, but as such there is little doubt that it was a compromising, tentative business, for a time at least far from a wholehearted abandonment of the one element for the other, rather as always a gradual transition, resulting in an amphibious existence. There could be no complete exodus and settlement of animal life on the land unless plants took part at the same time. But this must have happened as an equally gradual transition, perhaps of some of the seaweeds taking possession of a zone above highwater mark, so that in time they and their descendants could get to work on the inhospitable rocks of the continental margins, hasten their decay, and contribute humus in such a way that soil was at last produced. Only then could there be true land plants and true land animals.

Even at that remote time, measured in terms of the history of life rather than that of the earth itself, evolution had progressed to a surprising extent. The earliest fishes appeared in late Silurian times, and during the succeeding period, the Devonian, both salt waters and fresh fairly swarmed with them. But in the sea, apart from land animals that returned to it much later to become the whales and seals we know today, evolution went not much further, no further than the fishes of the present time. The sea, though an admirable medium both then and now for life, has its limits where further progress is concerned; and the tremendous significance of the migration of living things from the sea to the land is to be found in the fact that not until it had occurred could opportunities be found for the gradual development of the great succeeding classes – amphibians, reptiles, birds, mammals, and finally man himself. Much the same is true of plants. In the sea there are unicellular plants

* See table of geological ages, page 279.

innumerable, but apart from them seaweeds only. It was not until the land had become widely and securely colonized that the higher forms could arise – lichens, fungi, mosses, ferns, and finally the great host of flowering plants.

The ecologist can divide the peopled earth into the two great habitats of land and water, and to a certain extent he must. But in spite of the obvious differences between them, there are also fundamental similarities and these on the whole are of greater importance. In both elements it is plants that make animal life possible. In both it is oxygen that animals must breathe in order to live, whether the oxygen is dissolved in the water and taken in by means of gills, as with truly aquatic creatures, or as a free constituent of the air, as with land creatures making use of lungs. This does not mean that all animals to be found in or on the earth's waters breathe dissolved oxygen by means of gills. In the oceans there are the whales, the dolphins and the seals depending on oxygen taken in at the surface. In our rivers and lakes there are scores of creatures breathing free oxygen either for a part or for the whole of their life-cycle. There is a third parallel between life in the two elements. On land soil is a vital necessity because of the dependence of animals on plants, but soil does not enter into the lives of aquatic animals and this seems at first sight like a paramount distinction. But once again a close similarity underlies the difference. The creatures of both habitats require certain chemical substances, mainly phosphates and nitrates, in order to live, and these are conveyed to them through the agency of plants. The sea contains these substances in solution, available to a varying extent everywhere. But the soil also contains them, again in solution in the water that the soil is enabled to hold, and this soil water is the primary justification for the existence of soil so far as plants, and consequently animals, are concerned. A fertile soil holds water containing these substances, and the plants draw them into their tissues by means of their roots, converting them by an elaborate process into more complex substances available as food for animals. An infertile soil is deficient in or devoid of them. So in both elements we find

water containing mineral substances playing a part of primary importance.

It is clear, therefore, that ecology must begin with the great spheres of this planet, the primary envelopes of crust, water, air, and finally its ultimate concern, the envelope of life itself. These are the fundamental four, and though distinct, though of contrasted constitution in many important respects, they are nevertheless dependent on one another, renewing one another, constantly giving and taking. The atmosphere gives oxygen to the great waters both salt and fresh, gives rain, gives variations in temperature. Without the atmosphere there could be no hydrosphere as we know it. But the air also takes from the water, since the sea is by far the most important reservoir of that water-vapour which the air takes into its embrace, only to return sooner or later as rain. But if the rain has its importance where the sea is concerned, it has more for the land, for the crust of weathered and eroded rock where all the higher forms of life have their origin and their existence. The atmosphere makes possible the formation of soil, transforms it into the basis of life, but cannot do so on the one hand without the rain which it contributes, on the other without the humus provided by the plants. Nor is that all, since plants, themselves unable to thrive without both soil and rain, are vitally necessary to animals; while animals, as though mindful of their debt, provide not only the waste products of their bodies to make more nutriment for plants, but in dramatic and wholehearted fashion yield up those bodies themselves to replenish yet more the universal repository of mineral salts locked up in the soil.

So it goes on, this dynamism of give and take, this omnipresent nexus of mutual dependence. It goes on not merely between crust, air, water and life, not merely between plants and animals, but also between one plant and other plants, between one animal and other animals, until the strands of the web cross, bifurcate, and return upon themselves with a complexity to excite wonder and baffle analysis. This mutualism is the very stuff of ecology, a principle; one of two principles, of which the other is change. The web of things and the flow of things.

2

THE GREEN LEAF

I am in love with this green earth.
CHARLES LAMB

LIFE is of two kinds, plant and animal, and the distinction between them is a distinction in kind, something that we can see for ourselves. There are in fact a number of distinctions, most of them obvious enough; one, and that the most important, much less so. Among the obvious ones is that connected with movement. Animals move from place to place, plants on the other hand keep the same station from the fall of the seed to final decay. But this is soon seen to be an unsatisfactory distinction, since it holds good to a partial extent only. A very large number of animals remain in one place during their adult stage. These are the more primitive creatures found in the sea and in fresh water, such as sponges, anemones, barnacles. It is true also that unicellular plants are fully capable of moving about. Another obvious distinction is that plants are green, while animals seldom are. A third is that plants are much inclined to divide and branch, whereas animals are compact in outline. But these two are no more satisfactory than the first. The fungi are plants, but they are not green. Some animals, such as sponges and corals, are branched.

Functions of the green leaf

PHOTOSYNTHESIS. The only wholly satisfactory distinction is that which is the least obvious, and it has the great merit that all the others, for what they are worth, arise from it. This is the distinction with regard to food-supply, to nutrition. Expressed in the simplest terms it amounts to this: plants manufacture their food from simple inorganic substances, while animals are incapable of doing so and depend entirely on food that has

been manufactured for them by plants. This food-making carried out by plants is an exceedingly complicated process, but must be explained a little further. The fundamental concern, from which all their other food-making arises, is known as photosynthesis, which is the conversion of carbon-dioxide, present in small quantities in the atmosphere, into organic material such as sugar. This is carried out within the leaves by means of their green colouring matter, the chlorophyll, and the process can take place only in the presence of sunlight, making use of the radiant energy of the sun. This ability is the peculiar gift of plants, the supreme function that they perform in the scheme of things, without which animals, including man, could not exist. Plants take in also other simple, inorganic substances such as nitrates in solution from the soil, and these, combining with the products of photosynthesis, are further manufactured into yet more complex foodstuffs. It is on these organic foodstuffs – carbohydrates, proteins – that animals are wholly dependent.

This then is the primary distinction between plants and animals. Because of it plants are not required to move about, whereas animals must do so in order to find their food, in the form either directly of plants, or of other animals that are plant-eaters. Animals that are fixed in one spot during their adult stages have their food, either plant or animal, wafted to them, by the water in which they live. Because of this distinction too, plants are green, since chlorophyll is essential to the process. Animals possess no chlorophyll. Neither do fungi, but they make up for the loss by living as parasites on green plants or on dead matter. Finally, plants have a branching habit of growth so as to present as wide a surface as possible both to sunlight and to the penetration of their tissues by carbon-dioxide.

What is this so essential chlorophyll, sustaining life all over the earth, giving rise in its massed effect to that global verdure, which in a special sense is life's characteristic colour? We can say where it is to be found with far more accuracy than precisely what it is. It can be seen under the microscope, not

diffused through the whole plant, but as minute rounded bodies, known as chloroplasts, within the cells of a leaf. Beneath the outer skin of a leaf there is a row of elongated cells known as the palisade layer, and in these the chloroplasts crowd to the upper and lower ends when the light is subdued, but range themselves along the vertical sides when the sun is undimmed. They move with the streaming of the cell-protoplasm, but are endowed also with their own power of movement. Confessions of ignorance are always salutary and sometimes refreshing, and there is a wealth of ignorance where these processes are concerned. No one knows how it is that the chloroplasts move, and the details of the whole business of photosynthesis are still imperfectly understood.

An important product of the process is oxygen, which is given out. Apart from anything else then, plants tend to increase the world's supply of oxygen, imperative both for them and for animals. This can be seen quite easily, since photosynthesis is carried out as readily under water as in the air. Stand on the edge of a pond on a bright day and you may see rafts of floating, filamentous weed glistening with bubbles of oxygen. Keep fish in an aquarium and you can augment the supply of oxygen which the fish need and obtain otherwise from the air, by growing green weeds in the water. In the act of growing and of synthesizing their food they liberate oxygen.

RESPIRATION. But photosynthesis is no more than half the living-process of plants. The rest is respiration, which is essentially the setting free of the energy needed by the plant so that it may grow down through the soil and up into the air, and this is achieved by combination of the carbohydrates (sugars and starches) with oxygen, by their oxidation. This gives rise to carbon-dioxide and water, and at the same time releases energy. The release of energy is brought about by the fact that the carbohydrates before they are oxidized have a high content of energy, whereas the products of oxidation have a low content. The difference in energy between the two is the energy released and made use of.

We see therefore that photosynthesis, the first part of the process, is a building up of food-material and a storing of energy: the second part, respiration, is a breaking down and a release of the energy previously stored. The chemical processes of the two are reversed. Photosynthesis absorbs carbon-dioxide and liberates oxygen: respiration absorbs oxygen and liberates carbon-dioxide. Animals, as we very well know, respire no less than plants, and the process in the one is parallel with that in the other. But the differences are equally important.

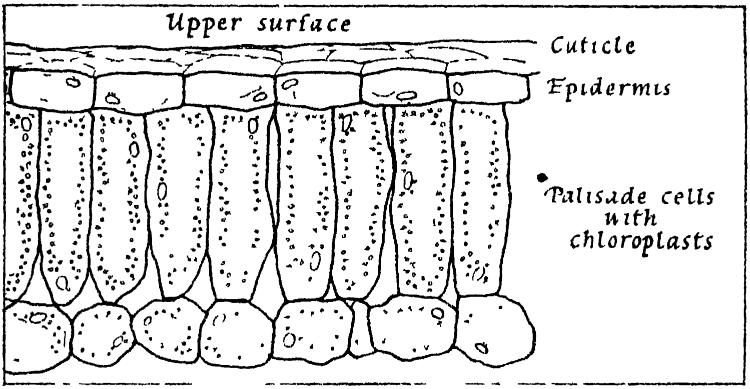

Figure 1. Section through a leaf showing palisade cells.

Plants in their respiration oxidize complex carbohydrates that they themselves have prepared by photosynthesis: animals on the other hand lack this power, and the carbohydrates that they oxidize during respiration have to be obtained by eating plants. But animals, or at least the higher animals, have carried respiration a stage further. By means of gills or lungs, coupled with a circulating blood-system, the gases are carried to every part of the body. In plants the exchange takes place in each cell independently.

The fundamental difference between the two forms of life

should now be clear. So should the reason why animals are wholly dependent on plants. Plants in a special sense are primary, and there is nothing impossible or contrary to nature in the thought of this world, or indeed some other, say for instance the planet Mars, as the home of life, but of plant-life only. A planet on the other hand as the abode of animals alone is out of the question. The same point can be emphasized in another way. Plants and animals are continually using up and breaking down substances with a high content of energy. How is it that the world's supply of these substances has not long ago become exhausted? There is only one answer: because of the ability of plants to renew the supply by photosynthesis. It is therefore quite impossible to exaggerate the importance of this great energy-producing engine, carried out in minute plant-cells existing almost everywhere in their uncountable millions. Let us not however give all the credit to the plants, for they after all are agents, transformers. The ultimate source of the energy they produce and that we animals depend upon, not only as food, but we human animals at least also as fuel in the shape of wood, coal, and oil, is the sun.

TRANSPIRATION. Since the life of animals is so closely bound up with the life of plants, animal ecology cannot be made into an isolated subject. It must be concerned with the ecology of plants as well. In the broadest sense this has already been touched upon. Something has been said of the relationship between plants on the one hand and sunlight and soil-water on the other. One more physiological point remains. Plants continuously give out water by a process carried out by the leaves which we call transpiration. It is in the form of water-vapour, capable of condensation, and is emitted through numbers of minute pores known as stomata. The total amount of water-vapour given off over an area well populated with plants is enormous. It has been shown experimentally that a single sunflower, in a growing season of eighteen weeks, gives off six gallons, which represents a bulk many times greater than that of the plant itself. This must mean that a large forest

contributes appreciably to the water-content of the surrounding air, and so can hardly fail to have an effect on the rainfall. Transpiration is of the greatest importance also to the structure of plants, for the emission of water is a loss that must be checked where water is scarce. As a result we find plants growing in dry regions possessing restrictive devices. Leaves are often coated with a waxy cuticle. The number of stomata may be much reduced. Leaves are frequently transformed into thorns, or in extreme cases absent altogether.

The ecology of plants

But my subject is not individual plants so much as their distribution, the way in which they grow in association with one another, and so the factors that modify, restrict or enhance their growth, in a word their ecology. These factors are of three major kinds, corresponding where land plants are concerned with the three great spheres mentioned in the first chapter: first those derived from the platform on which they grow, the rocks and so the soil; second those that are climatic; third those contributed by the plants themselves and by the animals as well. The last group is usually summed up as the biotic factors. These three must be dealt with separately, but it is of capital importance to realize that they are integral parts of a whole.

SOIL. The beginning of soil is the weathering of rocks, their splitting up into particles of varying size. But soil is far more than disintegrated rock. The particles provide the inorganic mineral substances that plants require, but in addition to these there is organic matter or humus, a product of the death of the plants that the soil supports. There is also air, and above all there is water. The paramount importance of water in the soil is that the mineral substances are dissolved in it, and so made available for the plants. It follows that anything influencing the amount of water in the soil is also of primary importance, and one thing that does is the size of the particles, which in turn

determines the size of the spaces between the particles. Relatively large interspaces allow free movement of water and air, relatively small ones restrict movement. But the particles and the interspaces must not be too large or movement will be too free and the mineral substances will be carried or leached away. A coarse, sandy soil is a poor soil. Finer sands, silt, or even clay, whose particles may be smaller than the hundredth part of a millimetre, will provide fertile soil. But clay under certain conditions becomes so impermeable as to be water-logged, as infertile as coarse sand. Loam, perhaps the best soil of all, is a mixture of sand and clay. Apart from all this there is the organic material, provided, as I have said, by the plants as they die. This is important because it greatly increases the water-holding capacity of the soil, and because it is that part where bacteria are constantly at work providing nitrogen and promoting the decay of plant remains, converting leaves, stems, and roots into that complex, amorphous substance that we call humus.

We must think of all this, not as something that rises spontaneously and exists statically, but like every other natural phenomenon, as a dynamic process, having a beginning and an end. The beginning, which was in truth less of a beginning than a renewal, can be dated, so far as Britain and much of the northern hemisphere are concerned, to the final retreat, the slow melting, of the great ice-sheets of the Glacial Period. This took place some 20,000 years ago. The Britain that then appeared, still joined to the continent but soon to be separated, was a howling wilderness of scratched and polished rock-surfaces, of thick, widespread deposits of gravel, sand, and of a tenacious, bluish clay, known as boulder-clay, a wilderness without a green leaf, except for a few mountain-top oases which had risen above the solid sea of ice. The work of soil-formation had to begin all over again, and under the steadily rising temperature of that happier time there was no delay. Invading inexorably from the south came the first colonizers of the dead glacial dust, bacteria, lichens, mosses. These pioneers were succeeded by ferns and grasses, which while

they lived drew upon the water that the embryonic soil was fast becoming capable of holding, and when they died yielded up their remains to form humus. More and higher plants gained a footing, working downwards with their roots. Earthworms made their invaluable contribution of mixing and turning, until the final result, vitally affected by climate, was a mature soil, a highly complex amalgam of dead and living matter.

CLIMATE. These great events in their slow development provided the soil, and at the same time the green mantle of plants, each stage of the process giving rise to its own type of vegetation, until at last there came the culmination, or as plant-ecologists call it, the climax. The nature of the climax depends entirely on climate. In a desert or semi-desert region it will be no more than a tenuous scrub, made up of plants adapted in various ways to live under arid conditions – long roots to tap deep sources of water, thorns to replace leaves, succulent stems in which moisture can be stored. In a region where the rainfall though heavier is still scanty and confined to one season of the year, the climax will be of the grassland type, with a few scattered trees – savanna, prairie, steppe Where the rainfall is comparatively heavy and well distributed through the year, there will be forests, equatorial or temperate.

Rainfall then is of the first importance All the same there was a good reason for beginning with soil, since that in a real sense is primary, the other factors exerting their influence on plants for the most part indirectly by way of the soil In fact it is not far from the truth to say that, apart from the question of deciding the nature of the plant-climax, it is really all a matter of soil, and that both climate and the biotic factors are of importance only because of their influence on the soil, chemical and physical.

But there are other things to be considered under the heading of climate. There are wind, temperature, and light. Wind plays a big part because of its influence on the transpiration of plants, and this can be appreciated most easily by realizing that

so far as the action of water on a plant is concerned a balance has to be set up between the amount drawn from the soil and that lost by transpiration. Loss by transpiration must not be greater than gain by absorption. If this does happen the plant will die. Wind accelerates transpiration, with the result that in a prolonged gale, under conditions of soil and temperature such that the plant cannot make good the loss, the foliage withers. But this is an influence comparatively local in its effect. Temperature on the other hand has a more general effect because it is exerted, not on transpiration from the leaves only, but also on the soil over a wide area. When the temperature is high evaporation is correspondingly high, and the amount of water available to plants may be seriously reduced. It is perhaps labouring the obvious to say that high temperature helps to produce drought. A low temperature, to make a much less obvious statement, also produces drought of a kind, a sort of false drought. The reason for this is that below a temperature of about forty degrees Fahrenheit soil-water fails to dissolve the nutrient salts that plants need. Transpiration accordingly must be held in check, or be made to cease altogether, during the cold season. To do this, plants have perfected various devices. Annuals die off completely, relying on their seeds, lying dormant in the soil, to produce a fresh generation when the temperature rises in the spring. Perennials rely also on seeds, but the plant itself continues to live, as it were in hibernation below the level of the ground. Those perennial plants that we know as deciduous trees, though continuing to live above ground, shed their leaves on the approach of winter. Light too has its importance, but that can be considered in the next chapter when the principle of dominance is described.

BIOTIC FACTORS. Last of the three groups is that concerned with life itself, both plant and animal, and here once more the intermediary is the soil. It is not a matter of the influence directly of plant on plant so much as that of plant on soil, and by way of the soil on other plants. Similarly the life, and more particularly the death, of animals deeply affects the soil and

so the growth of plants. This influence, in its most basic and widespread sense, has already been explained: the formation of humus, that complex organic substance produced by the

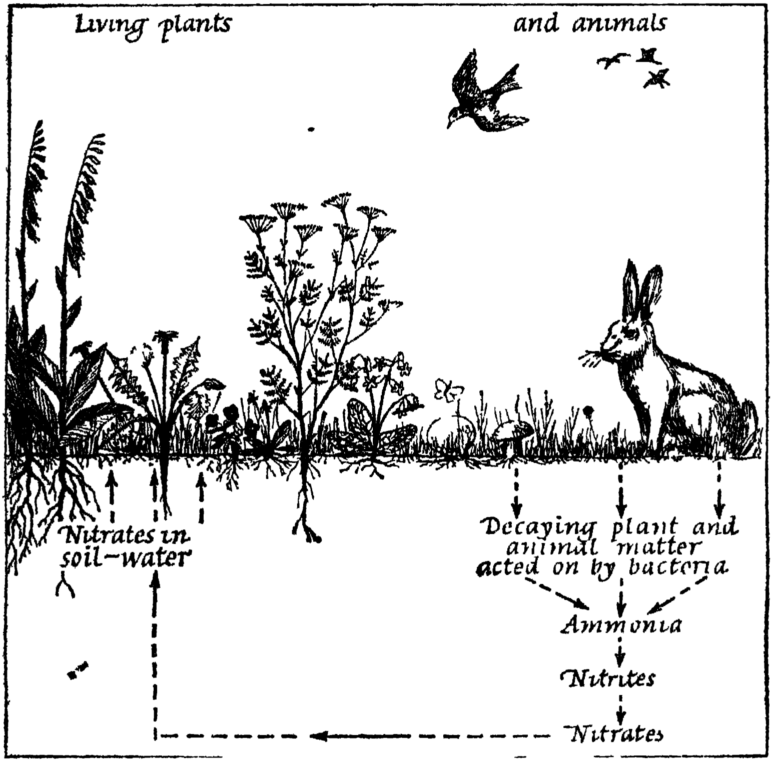

Figure 2 The nitrogen cycle

decomposition of plant and animal matter, giving the soil its dark colour, helping to retain water, building up a reserve of nutrient salts dissolved in the water and used by the plants.

But the soil does much more than contain the products of the decomposition of living things. It teems also with living things of its own. Of these the most important are the bacteria, themselves plants of a sort and having a highly important part to

play in this complex process of serving the interests of life. First to be considered are the nitrifying bacteria, carrying out what is known as the nitrogen cycle. When plants and animals die they return to the soil the complex organic substances on which they fed when alive and which built up their bodies. These, and among them the excrement of living animals must be included, are seized upon by bacteria of more than one kind and broken down by oxidation first into ammonia, then into nitrites, and finally into nitrates, available as food for the green and growing plants. This is a chain-reaction, or more accurately a closed circle of many links, by which the bacteria and the green plants between them convert nitrates by a long, complicated chemical process, back once more into nitrates. As well as the nitrifying bacteria there are others, the nitrogen-fixers, whose function it is to enrich the soil with further supplies of nitrogen, this time from the air. Some live freely in the soil, others in swellings on the roots of plants such as peas, beans, and clovers, which is the reason why plants of this kind play so important a part in the rotation of crops.

Nor must the earthworms be forgotten, since they have a profound influence both on the structure and composition of the soil. In Britain there are some twenty-five different species, and estimates of their abundance vary from one to three million to the acre. All of them swallow soil to find their food, while many set it free again at the surface in the familiar casts. It has been calculated that these casting species, in a heavily populated acre, may bring to the surface in this way, as much as twenty-five tons of soil each year. In addition to this it is known that they pick out organic matter for their food, while some draw leaf-fragments and twigs down into their burrows. This means a prodigious amount of mixing and turning both of the mineral and the organic constituents of the soil which cannot fail to improve its tilth. Worm casts, scattered over the surface, are known to be particularly rich in nitrates and other valuable minerals.

3

HABITAT AND COMMUNITY

> Nature works on a method of all for each
> and each for all.
>
> EMERSON

TO point out the way in which living things work in the interest of other living things, while at the same time going about their own occasions, is to stress the unity of nature. The formation of humus, by which plants provide other plants with organic matter; and the nitrogen-cycle, by which bacteria break down this organic matter so that the resulting nitrates become available to the plants, are two notable and closely linked examples. Photosynthesis and the respiration of plants are two more. Yet another is transpiration. In all these, not plants only but animals take their share and make their contribution. They are fundamental and world-wide. Wherever there is life on land they are in operation, ceaselessly and cyclically. Wherever there is life in the sea and in fresh water they operate, with inevitable modifications, also. Because of them the whole earth is a habitat fitted for living things, a habitat of infinite diversity, yet at the same time dovetailed into basic unity. This means that the one great habitat which is the surface of our planet is divided into smaller, but still from our point of view very large, natural regions, each of which is a major habitat with plant-forms and animal-forms characteristic of it and adapted to its conditions. Each is a dwelling-place with its rightful inhabitants, and these are of two kinds, a plant community and an animal community.

The water habitat

It is perhaps reasonable to begin with the sharpest division of all, that between water and land, though as I pointed out in the

first chapter, it is probably true that the resemblances between them as abodes of life are of greater importance than the differences. Nevertheless the distinction to us as land animals is clear-cut and of major importance. To living things everywhere one factor is bound to be of the utmost importance and that is the extent to which their habitat is subject to change, whether or not it provides a relatively constant environment. It is true also that change is of two kinds, that from place to place and that from time to time. Each in its own way is important, and the reason for mentioning this here is that the greatest of all water environments, the sea, is a habitat far less subject to change than any on dry land. From one part of 'the great salt deep' to another there are considerable gradations: those caused by differences of temperature, which are largely a matter of latitude, those caused by currents whose effect is to complicate variations of temperature, those depending on differences of salinity.

It is in temporal changes that we find a much more striking degree of constancy. Seasonal changes of temperature, for instance, affect surface waters only. The vast bulk of oceanic water never varies, so far as we know, from a temperature a few degrees above freezing-point. The sea is an environment not only intensely cold but intensely dark as well, so that plants, except for the seaweeds of the continental shelves, are found at or near the surface only, where there is some degree of both warmth and light. These facts are not true of the world's fresh waters, since they, even the largest of them, are so much smaller in extent. Fresh waters are deeply affected by frost. They, or at any rate their margins, are also subject to drought. Their shores may be reduced to dry, cracked mud. Both of these are eventualities to which plants and animals must adapt themselves, and there is little doubt that they have played an important part in the changes undergone by plants and animals themselves, in their evolution.

Natural regions of the land habitat

Conditions on land are vastly different where change is concerned. Spatial diversity occurs almost everywhere, temporal much more over some parts of the earth than others. The great natural regions of the geographer are the major spatial changes and we look upon them as permanent. Seasonal changes occur within most of them. If the earth's surface were solely of dry land the natural regions would be traceable as zones running east and west, parallel with the equator, but oceans and mountains break up this zonal formation. Even so, because of the size of the continents, it is not unreasonable to refer to them as zones. Owing their existence entirely to climate and not at all to rock-formation, they are distinguishable because of the angle of the sun's rays, varied according to latitude; because of distance from the sea, affecting both temperature and rainfall; because of exposure to prevailing winds. Each one supports a plant community in the widest sense in which that phrase is used, each plant community gives sustenance directly or indirectly to an animal community, again in the widest sense. Each one merges by slow degrees into the next. Each one, considered as a habitat for living things, is divisible into a very large number of smaller habitats.

THE EQUATORIAL FOREST. It is logical to begin at the centre and to work outwards, and in this instance the centre is the equator and to work outwards is to travel towards each of the poles. For the great natural regions, in so far as they form zones, are traceable as two sets of zones, the one stretching north, the other south of the equator. Since the proportion of land to sea is much greater in the northern hemisphere than in the southern, the zones are far more marked in the first than in the second. There is another reason for starting in the centre, for it is here on each side of the equator that we find the great equatorial forest of the Amazon Basin, the Congo Basin and the Malay Archipelago; and this type of forest presents a striking parallel with the ocean deeps as an environment for

life, in that of all the natural regions it is the one least subject to temporal change. In the equatorial forest (Plate 1a) there are no seasons. Climatic conditions vary scarcely at all from the beginning of a year to its end. At all times the rainfall is heavy, humidity is high, temperature is high. The result is a forest luxuriant, sombre and perennially green. In these hothouse conditions plants, from mosses, fungi and ferns to tree giants 200 feet and more in height, run riot. There is almost as much plant life growing on and around other plants as independently and self-sustaining. Festooning lianas loop from tree to tree. Branches are furred with epiphytes – ferns, bromeliads, orchids – plants, that is to say, rooted on living hosts but drawing no sustenance from them. Since there are no seasons governed by climate, there can be no corresponding seasons of leaf-expansion, flowering or fruiting, such as we in temperate latitudes know so well. Each plant undergoes its life-cycle in a season of its own, adapted to a constant environment. Through so dense and unchanging a tree-canopy sunlight penetrates fleetingly here and there, and there broods in consequence a perpetual twilight, a green shade if ever there was one, with the result that the floor of the forest is for the most part free of undergrowth, since only a few shade-loving species can tolerate so low an intensity of light. It is a world deficient also in colour, or more accurately dominated by one colour only, green in every conceivable shade, the rare and resplendent flowering of orchids for instance unfolding itself high overhead, where direct sunlight has a chance of falling.

In an environment such as this, supporting a plant community more varied and luxuriant than any other in the world, we would expect to find an animal community corresponding in both respects. There is no doubt that it exists, but it is far less visually in evidence than the plants. Insects of course teem in their millions but even they, or many of them, have to be searched for, since they conceal themselves, either directly under cover, or by protective resemblance to their background. During the hours of daylight their voices are hushed, as are those of most of the forest's other denizens. The notes of

birds sound only occasionally, while other animals – reptiles and mammals – move in silence and furtively, if at all, through the miles of massed tree-canopy to which they are so intimately adapted. But at night the animal community comes into its own, when the impact of massed vegetation no longer makes itself felt and the darkness throbs with an orchestra of uncoordinated strings, wood-wind and percussion.

THE TROPICAL GRASSLANDS. The traveller moving north or south from the equatorial zone finds himself in time in a region where rain no longer falls throughout the year. A dry season intervenes and grows steadily longer as the equator is left behind. A zone is eventually reached where the rainfall is no longer sufficient for the demands of a forest and the dominant plant-form is grass. This is the zone of tropical grasslands or savanna (Plate 1b). Trees, no longer massed, are scattered in a park-like growth, a scrub of feathery, flat-topped mimosas, or occasional, bulbous-trunked baobabs. There may be forests, but they will be confined to winding corridors clinging to the banks of a river. Rain falls in the summer months only, when the wide plains clear across Africa quickly become flushed with green. Within a few weeks clumps of tall grasses, tufted and plumed, rise everywhere, and for a season there is abundant grazing for a host of hoofed animals, for this, in Africa at least, is the game country, where herds of antelopes move, or for the most part once moved, like cloud-shadows over the plains. With the passing of the autumn equinox the rains die away and the grasses with them, scattering their seeds, until before long what once was green becomes sere and baked. Similar conditions, supporting animals with similar ways, though differing widely in species, are found in Northern Australia, in the Orinoco Basin and the Matto Grosso of Brazil.

THE DESERT. The reach of the summer rains, to which the grasslands owe their existence, is limited towards the north. In the same way and for a similar reason, the reach of the winter rains of the Mediterranean Basin is limited towards the

south. Between these limits there stretches a wide gap where rainfall is negligible, even non-existent. That gap, so far as Northern Africa is concerned, where the continental land-mass is of huge extent, is covered by the Sahara Desert. South of the equator also there is desert, but the continent here is narrower, trade winds from the Indian Ocean bring rain to the east coast. As a result we find the far smaller Kalahari.

As a habitat for plants the desert is naturally exacting in the extreme. To exist at all plants must adapt themselves rigidly to make the very most of such small amounts of water as they can find, and it is here that they have evolved those devices to restrict transpiration or prevent it altogether, those thorns which are modified leaves, those long root-systems reaching down to tap sources of supply many feet below ground-level, that succulence which is water stored up in the tissues. To these conditions of general aridity animals too must adapt themselves, as also to extremes of temperature far greater during the twenty-four hours of the day than during the twelve months of the year. They burrow underground, they hide under stones to escape the fearful heat of the sun and the bitter cold at night. Dew is certain to be of greater importance to them than more usual supplies of moisture, and they take full advantage of rare downpours of rain when seeds, dormant in that inhospitable soil, germinate almost visibly and for a brief spell the desert blossoms like the rose. Most of them are adapted in another way: desert animals are for the most part desert-coloured.

The Sahara is by far the biggest desert in the world, but for all its immensity it is really no more than a part of one yet more immense, stretching from Cape Verde in the extreme west of the African continent clean across to the Red Sea, from there across Arabia, and with a northerly slant to include Iraq, Persia, Baluchistan, as far as the easternmost fringe of the Gobi. Within that great area, straddling two continents, conditions vary widely, and there are in fact deserts of several kinds: rock-deserts, sand-deserts, mountain-deserts. Fronting the Pacific Ocean, along the coasts of Chile and Peru, stretches the glaring ribbon of the Atacama. There are mountain-deserts in

the south-western United States. Most of Western Australia, and the whole of the interior of that continent, are desert.

THE MEDITERRANEAN LANDS. Southward of the desert zone in the southern hemisphere there stretches a great girdle of ocean with no more than meagre margins of land. But in the northern hemisphere the continents swell northwards, radiating outwards from the pole, and there are other regions to be taken into account. Merging into the desert is that zone of winter rains to which the Mediterranean Sea gives its name. These rains come from oceans lying to the westward, and so long as no mountain barriers intervene, as they do both in North and Southern America, the regions with a Mediterranean climate stretch far to the east. As an environment for living things these regions are not unlike the savanna, with the rainy season a winter instead of a summer one. Conditions in summer are extremely arid and plant-life, like that of the desert and the savanna, must adapt itself to drought, must become as is said xerophilous. It is in this zone that we come across the deep and widespread influence of man over centuries of organized, communal existence. Most of the vegetation in this region, at least in Europe, is either of the cultivated kind, or at best all that is left, over wide areas scarcely anything at all, of what was once forest. For it is the habit of man, by far the most destructive of all animals, to divest the earth of its natural cover, to cut down trees, to plough up grasslands, to upset the great cyclical processes of nature, and all too often to make a desert and call it, not peace, but civilization.

THE MIDDLE LATITUDES. Northwards again we come to the belt of permanent, moisture-bearing winds, the oceanic westerlies, bringing well-distributed rainfall both to the margins of continents and, if no mountain barriers stand in their way, far into the interior. The result once again is forest, deciduous and broad-leaved in the south, evergreen and needle-leaved in the north. In the centres of continents, where rainfall is comparatively scanty, there are grasslands of the temperate sort –

the prairies of North America, the steppe-lands of Russia, the pampas of Argentina. Both in North America and in Europe most of the deciduous forest has vanished under the axe, and a highly artificial countryside of arable fields, enclosed pastures, and vineyards has taken its place. But far to the north there still stretches a great global belt of sombre, coniferous forest, from British Columbia across Canada to Hudson's Bay, then from the Scandinavian countries across Finland, Russia and Siberia to the shore of the Pacific.

Each of these, the two kinds of forest, the temperate grass-lands, is a great habitat of plant and animal life. Of the three by far the most impressive is the great belt of coniferous forest, if only because it is the least encroached upon by human activities. Its southern fringes are continually whittled away by the demands of the timber and paper trades, scores of square miles are destroyed annually by fire, but for all that it stands virtually intact even today, one of the few remaining wildernesses, a sanctuary to inspire awe and bring refreshment. Comparison with that other surviving wilderness, the equatorial forest, is inevitable and presents a few features common to both as well as many contrasts. Both are forests, both are robed in unvarying verdure; but the trees are vastly different, not merely as species, to the extent that no kind of tree grows in the one and in the other, but also in their distribution within each. The equatorial forest consists of hundreds of species and it is the exception for more than a very few of the same kind to grow adjoining one another. The northern forests on the other hand are made up of no more than a dozen or so kinds, and their way is to group themselves in far-spreading, homogeneous stands of spruce, hemlock, pine, or balsam fir. This means that change is a marked characteristic of the coniferous forest, and change of both kinds. Spatially you pass from one stand to another, seasonally from hot, mosquito-haunted summers to winters of heavy snowfall with temperatures down to twenty or even thirty degrees below zero, with all that this means to its animal inhabitants.

THE TUNDRA. One great natural region remains to be mentioned, that which lies beyond the tree-line, polewards of the forest, the arctic tundra. It is as accurate to say tundra only, for though a great continent encircles the South Pole, it is blanketed by ice and there is no comparable region in the southern hemisphere. The tundra, stretching from Alaska to Labrador, then from Lapland across Siberia to the Bering Strait, is in general low-lying. If it were mountainous it would be ice-covered like the Antarctic continent and like Greenland in the north. The subsoil is frozen at all times, the surface soil, so far as there can be said to be any, for nine months of the year. Travellers at first are apt to be overwhelmed by its dreary monotony, but with closer acquaintance find that it is by no means lacking in charm – the clear air, the huge horizons, the gentle undulations tinted in duns and greys, but surprisingly varied within its sombre limitations. Naturally it is treeless, or at best matted with dwarf willows, close-pressed to the ground, reaching out on all sides through the thin soil. For the rest during the greater part of the year mosses and lichens, pioneers elsewhere, are here almost the sole settlers on the forbidding land. In winter, at this latitude nine months long, blizzards rage wantonly, punctuated by interludes of calm; but in the spring a wonderful transformation takes place. The temperature rises, the snow melts, the rivers clash and grind with slabs of ice churning seawards, and the barrens blossom with a wealth of alpine flowers of the sort found elsewhere many thousands of feet above sea-level. During the brief summer they complete their life-cycle, set their seed, and die. With them come insects, most notably mosquitoes in droning clouds. Flocks of migrant birds arrive and the rejuvenated wilderness echoes with their fluting. There are foxes, hares, and hosts of trekking caribou. The tundra, for all its appallingly severe conditions, for a season at least, becomes an environment that teems with its own living things.

These are the major divisions of the earth's surface, all of them of great extent. They are very much the concern of the ecologist whose business it is to study the plant communities

and the animal communities that they support. But their vastness is an embarrassment. Relationship between plant and plant, between animal and animal, relationship between each of the two and the other, to say nothing of the all-important influence of climate and soil, are complex beyond imagining. Fortunately for the ecologist, he is not called upon, in the earlier stages at least, to give his attention to any one of the great regions as a whole. Because of the limitations of the human mind it would indeed scarcely be a possible undertaking at any time. What saves the situation, paradoxically enough, is that very vastness itself. The natural regions are in fact so enormous from the human point of view that conditions over any one of them could never be the same, and as a result, while keeping in mind the general similarity in the broadest sense, the ecologist can fasten his attention on one or more of a very large number of minor regions, minor habitats, within the major one. These sub-regions are not only numerous, they are also variable both in size and in character. It is quite possible, it is indeed frequently advisable, to study the smallest of them. Many would say the smaller the better.

The diversity of habitats

What is it that causes this diversity within broad similarity? It might be supposed that it is climate if only because the major regions are climatic regions. So it is in the last analysis, but differences of temperature, humidity and rainfall, and so of soil conditions, are brought about by differences of relief, by the diversification of the earth's surface into mountain, hill, valley and plain. The whole thing could be summed up in the one word slope, for it is this that causes variations both great and small in climate and soil conditions, and so in the life that the soil supports, from one part of the earth's surface to another. Variations in rock-structure on occasions play an important part as well.

Broadly speaking a climate becomes more severe as altitude above sea-level increases. Temperature drops, rainfall increases,

winds are more keenly felt, and this has a marked effect on plant life. In our own mountainous districts for instance oak-forest, where any of it has been left standing, clothes the lower slopes. At about the 1,500-foot contour-line trees give way to sparse scrub, and scrub in its turn to grass or ling. The result is a marked zonation, even over our modest mountain slopes. Where the great mountain ranges of the world are concerned, this zonation becomes much more noticeable from sea-level up to the snow-line. Another and related influence is that of aspect. In the northern hemisphere southward-facing slopes receive a higher concentration of the sun's rays than northern, and for that reason support a higher proportion of plants that are intolerant of shade.

Slope affects also the nature of the soil, since gravity and the action of running water combine to carry soil from hillsides down into the valleys. We can trace this same influence of slope over much wider areas, for what is it but slope that causes rivers to flow, with all that that means in the way of river-erosion, producing marked differentiation into a steep and rocky upper-course, with sharp gradients and a swift current; a middle course, with a slackening current and the beginnings of a flood-plain; and lastly the lower-course, where the river flows sluggishly in snaking meanders over a wide and level plain. Rivers alone are powerful agents of diversification. Then there is the important influence of the water-table, the level that is to say below which the rocks are permanently saturated with moisture. As a general rule this level tends to be nearer the surface beneath valleys than beneath hills, and this can hardly fail to show its influence on plant life. Finally, and once again to a large extent a matter of slope, there is the appearance of untenanted surfaces for plants to colonize. This may happen through the action of rivers depositing silt, of the sea forming mudflats, of the wind heaping up dunes of sand against some inland obstruction.

All these help to demarcate minor regions within major ones, smaller habitats, each with its plant and animal community, within bigger ones. The influence of rock-structure

lies in the same direction, since what is soil as the geologist reckons it but rock? But rock-structure in its own right, apart from gravity and running water, may well be important. One of the commoner kinds of rock is limestone in various forms, and the lime that it contains wields a most noticeable influence on plants, some demanding it, others perishing if they come in contact with it. To cite an example familiar to many, in the West Riding of Yorkshire the high hills of Ingleborough and Penyghent are built mainly of limestone, carpeted verdurously with grasses and all manner of lime-loving flowers. In contrast, much of the lower levels, mantled with glacial drift, are relatively free of lime, have an acid soil and a flora consisting of ling, which dominates other plants, often to the extent of excluding them altogether, and will not grow on the limestone uplands.

Plant communities

It is because of all this, because of the great climatic natural regions, of the smaller climatic sub-regions contained within them, of differences of relief and differences of rock-structure, that plants do not grow at random, but in communities or associations, each one characteristic of its habitat. Within that habitat the plants are subject to certain interacting influences, chiefly of soil and climate, and it is these influences that cause the habitat to exist. These two are the primary factors, but there is another in a sense secondary, since its effect is not to bring the habitat into existence so much as to modify it in various ways. It is a set of factors rather than a single one and comprises those that depend on the plants and the animals themselves. They are the life or biotic factors, and of all of them the most profound and far-reaching are those for which man is responsible, this of course applying only to those countries having a long history of human settlement. In Britain for instance man has transformed a wilderness of forest, interspersed with grassland, into an ordered garden. In many places he has not influenced habitats: he has simply wiped them out. But apart from this sheer destruction, his influence

in the way of deforestation, cultivation, grazing, fire, is seen everywhere. But this book is not concerned with human activities, except where they cannot be evaded: its concern is with nature, and for that reason the structure of plant communities and their associated animals will be considered, in so far as that is possible, as though man did not exist.

What are the biotic factors exercising their influence on plant communities and on the animals inhabiting them? In the first place it must be made clear that within any one of these communities plants do not grow at random, in unrestricted competition with one another, any more than they do over the earth as a whole. In all of them there is organization, a graded hierarchy, so arranged that the severity of the struggle to exist is restricted by what after all is a form of cooperation The principle of dominance is the first consideration, by which one or more species, frequently one only, exercises primacy over the others. The dominant species gives its name to the community. We speak of an oak-wood, a heather-moor, a reed-swamp, and in each of these the subordinate plants exist by sufferance of the dominant. Not only do they live subject to the restrictions imposed by the dominant, they are found there because they can do so The dominant plants are those that make the greatest demands on the resources of the habitat. the rest make the most of those that are left. But even at that the struggle is far from being unrestricted. There is a sharing of gifts. The dominant plants are frequently the tallest, usually the most numerous. The others must be tolerant of shade in varying degrees, showing the degree of their tolerance by a sort of stratification, oak-trees, for instance, in an oak-wood at the highest level, shrubs such as hazel or hawthorn considerably lower, herbs such as primroses, bluebells, anemones forming the ground-layer. There is a sharing also of moisture-resources by a stratification of another kind, the roots of the oaks probing far down, relying mainly on moisture rising from below, those of the shrubs to an intermediate level, those of the herbs near the surface, making use of the water that falls as rain. The dominant plants need not, of course, be trees. They can be

shrubs or even herbs, and it is climatic conditions almost solely that determine which of the three they are to be. The species of tree, shrub, or herb on the other hand is a matter of geography, though that too is largely climatic. As for the subordinate plants, their abundance and arrangement are under the

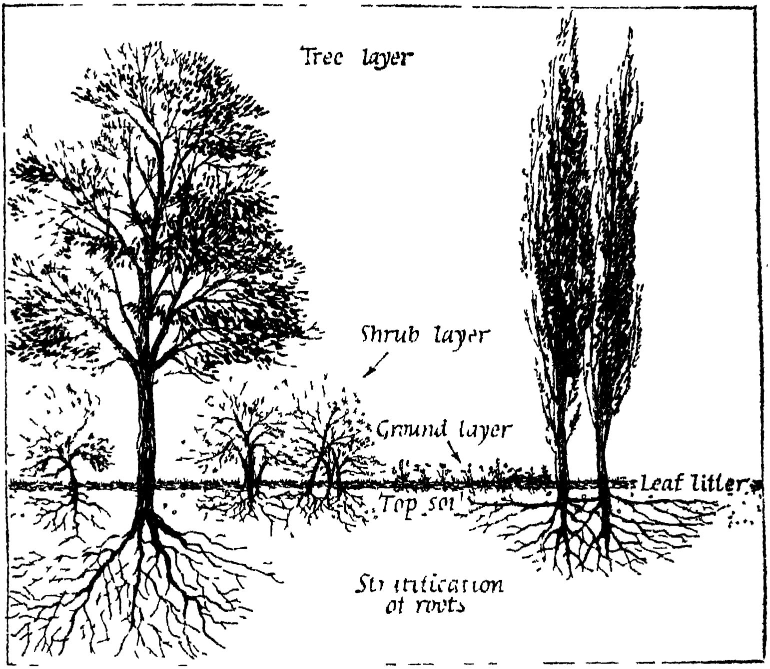

Figure 3. Stratification above and below ground in a wood.

dominion of the dominants entirely, not only as to the amount of light they permit, but in the shelter they provide, the modifications of temperature and humidity they give rise to, and the supply of soil-moisture they allow. The dominants also exercise a profound influence on the composition of the soil, because they are the chief producers of humus.

Since there are smaller climatic sub-regions within any of the

great natural regions, so there are smaller plant communities within larger ones. In fact, seeing that the natural regions are themselves plant communities on the largest scale, this is not so much a case of two things being parallel as identical. A wood is a plant community of the kind known as an association, but we speak of different kinds of wood, oak-wood, ash-wood, beech-wood, each a community designated by the species of the dominant. In the great coniferous forest belt of the northern hemisphere this same arrangement is seen in the way trees tend to associate in stands of the same species, and we find what amounts to pine-woods, spruce-woods and the rest as component parts of the great plant community which is the forest-belt as a whole. In the equatorial forest conditions are somewhat different and we will not find minor communities of quite the same sort, or if we do then the dominant plants may consist not of one species but of several. This splitting up of communities can be carried a stage, if not several stages, farther. Within, say, an ash-wood or a stand of hemlock in the coniferous forest, local differences of soil-structure or of moisture-content will certainly give rise to quite narrowly defined communities, possibly of shrubs or even of herbs, each with a dominant species of its own.

In a restricted area such as the British Isles, so widely influenced by human activities, the broader types of plant community are many. A recent writer on plant life in this country makes the following classification. Separating natural or semi-natural communities from natural ones, he makes important distinctions between various kinds of coastal community – salt marshes, sand-dunes, shingle-beaches, rocks and cliffs. Then come aquatic communities – ponds and lakes on the one hand, rivers and streams on the other. Marshes are to be distinguished from fens and bogs; marshes with an inorganic, muddy foundation, fens based on peat, more or less alkaline or lime-containing, bogs also based on peat but acid or deficient in lime. Next come various kinds of grassland, separable also by the amount of lime in the soil-water. Heaths and moors form a separate group, as do the woodlands of some six

different types. Finally there are mountain communities. Another botanist might draw up a somewhat different list but the differences would be slight, confined mainly to the way in which one or more of the larger categories were divided into smaller ones.

Dependence between plants and animals

Up to now it is plants that have received the greater share of attention. The reason for this is the absolute dependence of animals on plants. It was necessary to lay the foundations, and from there to work upwards into the complicated structure of animal life rising from these foundations. These are the two kinds of life and the two kinds of community. Ecology in the broadest sense is the study of both and of the strands that bind them together. Because of the marked distinctions between the two kinds of life there are plant ecologists and animal ecologists. Their separation to some extent is inevitable, since each is a subject big enough to claim the attention of a specialist; but in spite of this the one can never be divorced from the other if anything approaching a complete understanding of the wonder and complexity of life as a whole is to be achieved. The animal ecologist must know something, the more the better, of plant ecology. The converse also holds good, if perhaps to a smaller extent. So from this point onwards, while attention will be given mainly to animals, plants too will receive their share. We cannot have the one without the other. In the meantime it will be logical to enlarge upon this vital dependence.

The more fundamental reasons for the dependence of animals on plants have already been dealt with, a matter of food-supply, in one word, photosynthesis. All animals without exception, man included, are in the last analysis vegetarians. That is primary, but there are other, secondary, forms of dependence, and perhaps the most important of them can again be expressed in one word – shelter. It is part of the munificence of plants, particularly of plants grouped into communities, to

mitigate the severity of climate, to set up circumscribed micro-climates differing in a number of ways from the general climate of the natural region in which they grow. In a cold climate the temperature within the shelter of a plant community will be slightly higher than that outside. In a hot one it will be lower: it is cooler within the shelter of a wood than outside. There is also atmospheric humidity which plants augment by their transpiration, and this is a highly important matter for all but the higher forms of animals, for worm-like creatures, many insects, for molluscs, amphibians, and reptiles, to whom desiccation is an insidious and ever-present danger. Perhaps the most striking example is to be found on a rocky sea-shore at low tide, where dense wet draperies of seaweeds of many kinds give shelter to a whole host of creatures, from sponges and hydroids to small lurking fishes. Without this protection all those creatures would die from exposure. Then there is light-intensity, harmful to some animals, and this too plants can modify. Finally there is direct shelter from high winds and drenching downpours. Apart from these climatic considerations, many animals rely on plants during at least one stage of their life history. We have only to think of the nests of birds, or of the host of insects working out the larval or pupal stages of their metamorphosis tucked away in some recess of woven leaves, cemented to a green-stem, ensconced among roots, or tunnelling under the bark of a tree. A semi-aquatic beetle known as *Donacia* has perfected a beautiful refinement of this sheltering technique. The copper-coloured adults can be seen in the spring on the leaves of bulrushes rising from the margin of lake or canal, but the larvae burrow into the succulent stems below water-level. Here they need air and succeed in finding it hidden in minute pockets deep within the tissue of the plants.

The debt, therefore, of animals to plants is beyond all computing, but dependence in nature is mutual more often than not, and it is a debt constantly and amply paid in more ways than one. The more fundamental method of payment has already been referred to, that yielding up of their bodies when

they die, so that bacteria can get to work and render down the complex compounds contained in them to simple nitrates, in this way made available to plants. In addition, as farmers and gardeners know, there is manure, rich in nitrogenous substances. These two methods combine to make a payment of the debt so wholehearted that we might suppose it to be enough and more. In fact there is another return, quite distinct and almost equally indispensable to the plants. The truth is that they depend to a very large extent on animals for their successful propagation, so much so that it is safe to say that if it were not for this form of assistance plants could never cover the greater part of the face of the earth as they do.

While it is true that among plants non-sexual methods of reproduction by suckers, layering and the sheer proliferation of root-systems, are far more frequent than among animals, sexual methods play a major role. Another distinction is that the sexes are more often found together in a single organism. Self-pollination, that is the conveyance of pollen from the stamens to the stigma of the female organ within the same flower, is by no means uncommon. In spite of this, cross-pollination, or the carrying of pollen from plant to plant, has one great biological advantage in that it makes possible a far greater mixing of those hereditary factors, the genes, and so gives rise to more frequent variations which are the raw material of evolution. So much stress has been laid on this advantage that many plants have perfected devices, such as the ripening of the stigmas at a different time from that of stamens, to prevent self-pollination. That is a negative device. A surer and positive one is to increase the chances of cross-pollination. One way of doing this is to call the wind to their aid, a common method among plants that are tall and for that reason exposed to the wind, that is to say, trees. Another, less common, but made use of by some river-side plants, involves running water. But both of these are chancy and wasteful methods. Far better to enlist the cooperation of animals, offering at the same time some substantial reward for their trouble. So there has arisen, in the long course of evolutionary

history, that lovely reciprocating contrivance, the cross-pollination of plants by insects, by which many kinds of insect, particularly bees, but wasps, flies, beetles, butterflies, and moths as well, are offered an inducement to visit flowers. Many of these insects are at liberty to eat pollen since there is plenty of it. Others are attracted by the nectar secreted by most flowers, while others again, the honey-making bees for instance, delight in both pollen and nectar. All of them in the course of their burrowing, exploratory visits are certain to become liberally dusted with pollen and consequently to convey it from flower to flower and from plant to plant.

How this expedient first arose we can scarcely even guess, but we do know that it was a huge success, so much so that there is little doubt that those two great lines of development which fill the world with so much beauty, flowering plants and winged insects, progressed in tandem, evolved in intimate cooperation, each one giving rise to the other over a lapse of time amounting to some 200 million years. Throughout that time many an exquisite adaptation has been perfected in the structure and outward appearance both of flowers and insects. Among insects we find, for instance, the long proboscces of bees, butterflies, and moths, long in precise relationship to the spurs and pockets of the flowers where the nectar is to be found. To this arrangement also the bees owe the furriness of their bodies, a furriness made up of branched hairs, all the better for the entanglement of pollen-grains. On their legs are the pollen-baskets, crammed so often with a paste of pollen and nectar.

As for the other side of the medal, the adaptations among flowers, designed on the one hand to attract insects, on the other to make easier both the extraction of pollen and the subsequent placing of it on the stigma of another flower, it is not too much to say that the almost infinite variety in the shape and structure of flowers, their fragrance and their colours, owe their existence to the paramount importance of insect visitors. Wind-pollinated plants have flowers so inconspicuous that frequently we are unaware of them. Why should they be

conspicuous? Of what use to the undiscriminating wind are gaudy petals, alluring scents, elaborate devices for the safe and specialized conveyance of pollen? This is a big subject. To deal with it adequately a whole book would be needed. Perhaps enough has been said here to make clear that in the whole world of nature there is no more wonderful instance of mutual dependence.

The pattern of life

The pattern of life everywhere on the surface of the globe is in the form of a sort of mosaic made up of individual tesserae, each one consisting of a plant community together with an animal community, living directly or indirectly upon it. This is true even of those regions where man has left his mark, on occasions to the extent of wiping out entirely everything that we call natural. After all humanity is part of the pattern. This analogy of a mosaic is useful up to a point, but like nearly all analogies it breaks down when closely examined. It would be grossly misleading if the very limited extent of its application were not clearly understood. A mosaic when viewed as a whole achieves a comprehensible design, each of its separate units contributing something to the total effect. So far the parallel can be allowed to stand, though in nature the relationship of the parts to the whole is incomparably more complex. It is when the individual parts are looked at as individuals that important distinctions at once appear. The parts of a mosaic are detachable, have sharply defined boundaries, are of simple homogeneous construction, and are self-contained. The tesserae of the mosaic of life have none of these qualities. They are indissolubly linked both with one another and with the whole, merge gradually as a rule, are exceedingly complex, far from homogeneous and seldom self-contained.

These considerations are of the first importance, and the last of them must be examined further. In the natural world the unit is the habitat with its two components, plant and animal. The plant community consists of many different kinds of

plant, usually with one of them occupying a position of dominance in numbers and in size. The animal community also consists of more than one kind of animal, nearalways of many different kinds, and the principle of dominance, though present in a way, is of a totally different sort from that shown among plants. This will call for detailed examination later. The thing to be insisted upon now is that, while from one point of view the dependence of animals on plants cannot be too strongly stressed, since it is fundamental, from the point of view of the pattern of life it would be misleading to suggest that two different and adjoining plant communities would necessarily support two different corresponding animal communities. The two kinds of community, in other words, seldom exactly correspond. There is a marked tendency for animal communities to overlap one another, some species being common to two different plant communities.

The point can perhaps be made clear by saying that animals, considered in this way, can be divided into three categories: first those that are exclusive to a particular habitat, not to be found in a different one; second those that are characteristic of their habitat but fully capable of overlapping into one of another kind; finally a few highly adaptable species capable of ranging over a wide variety of habitat. The explanation of this distinction between the two kinds of life is fairly simple. Animals, or most of them, are capable of movement from place to place: plants, with a very few exceptions, are not. It is also true that animals are on the whole more adaptable than plants. To cite examples of the three categories: water-beetles will not be found in the grass surrounding their pond, but are exclusive to the pond and to other habitats of the same kind. House-martins on the other hand belong, so far as their breeding is concerned, to the habitat of the fields and houses of a village, but will frequently swoop over the pond and even dip into the water to catch water-dwelling insects. They are characteristic of both habitats. Certain kinds of two-winged fly are to be found in habitats of many different kinds. Not infrequently the situation is complicated when an animal belongs to one

habitat for an early stage of its life history, but to another for the succeeding stage. Dragonflies are exclusive to aquatic habitats so long as they are nymphs, but as soon as the stage of a free-flying adult is attained, become characteristic now of the air above a pond, now of the fields, woods, and even gardens surrounding it for a considerable distance.

Unity of the habitat

It is of the utmost importance to lay stress on the essential unity of any one habitat from the largest to the smallest. Climatic conditions and soil conditions, intimately bound up with one another, are responsible for the habitat being there in the first place, but it would be a capital error to think of it as a sort of container into which the plants and animals are introduced as its inhabitants. The plants are just as much a part of it as its climate and its soil. So are its animals. All four of the components are inextricably linked. They *are* the habitat, and without all four of them, within certain limits, no habitat can exist. A habitat without plants in direct or indirect association is unthinkable. This is true even of the black and frigid abysses of the sea, where no plants can live. Plants are found at and near the surface of the sea as diatoms in uncountable millions. There are many animals that use them as food, and these when they die sink into the abysses, where abyssal animals live either on their dead remains or on one another. It is, of course, true that there are parts of the earth's surface devoid of life, the snow-covered surface of the ice-cap of the Antarctic continent for instance, or a stretch of absolute desert so sun-baked and destitute of moisture that no plant can endure. But both of these, besides being barren of life, have no soil either. They have climate and no more. They are, of course, potential habitats. In the case of the desert area a very slight change of climate, even a single and rare shower of rain, such as is not unknown, would transform it for a time at least into an abode of living things. On the other hand, a very substantial change of climate indeed would be required to

mollify conditions sufficiently over any part of the Antarctic continent. Yet another point is worth making. In no habitat anywhere, so far as this planet is concerned, can there be animals without plants, but in theory it should be possible to find a plant community destitute of animals. In practice, owing to the enormous success with which animals have covered the face of the earth, it is doubtful if any such thing exists.

The size of habitats

The size of a habitat is an important consideration, particularly the enormous variation in their size, and the way in which a single example contains many smaller ones, each of these capable of yet further sub-division. An English oak-wood, for example, is a habitat, a plant community of a recognizable kind, depending on certain soil-conditions owing their existence to climatic factors measurable with some degree of accuracy.

From the point of view of the geographer, interested in natural regions, the oak-wood is so small as barely to come within his notice. From that of the ecologist on the other hand it is large, even if no more than a few acres in extent, contains plants of many kinds from mosses and fungi to oak-trees, as well as many kinds of animal from foxes and badgers to creeping things barely visible without a lens. The complexity of the relationship between all these living things is so extreme that it can barely be grasped in terms of the wood as a whole. Before he can hope to do so, the ecologist will have to split up this relatively major habitat into smaller ones, a process that is made easier for him because it has already been done by nature. As I have already pointed out, there is a three-tiered stratification among the plants into a tree-layer, a shrub-layer, and a ground-layer. Each of these is a habitat in its own right, with its own animal community made up of a few exclusive, many characteristic, and some widely ranging species which lawfully regard the whole wood as their domain.

The process of sub-division, when it has been done to that extent, is far from finished. In a sense each tree, shrub and

herb is a habitat, an ecological unit, and could be treated as such; but to do this would be wearisome to the point of madness and would mean endless repetition. A much more practical method was used by Mr Ernest Neal in a recent survey of an English wood. What he did was to divide the tree and shrub layers in the first place into leaves, buds and shoots, in the second into trunks and boughs, in the third into fruits and seeds, and in the fourth into roots. The ground-layer was split up somewhat similarly. On the surface was the layer of herbs, and here the principle of dominance came into play forming micro-habitats ruled by primroses, bluebells, dog's-mercury, and others. Below this was the layer of leaf-litter, and below that the top-soil. More minute sub-divisions could hardly be disregarded. A chance hollow in the trunk of a tree, where rain-water has collected, is a recognizable habitat, quickly colonized by unicellular animals, by rotifers and mosquito-larvae.

Examples of other habitats with similar sub-divisions and a comparable complexity could be cited almost without end. A pond in an English field is a habitat recognizable by everyone. Just as most people think of a wood as containing simply woodland creatures and woodland plants, so, perhaps even more so, do they think of a pond in similar simple terms. But simplicity is a word no more applicable to ponds than to woods. No two woods, no two oak-woods, are quite the same, and this is true also of ponds. But all kinds of wood and all kinds of pond have one thing in common, and that is a differentiation of habitats from one part to another. The general habitat of the pond must be divided by the ecologist into a number of minor ones. One of these is the surface of the water, with water-skaters and whirligig-beetles supported by the surface-film. A second is the mud of the bottom, heavily charged with decaying vegetable matter, and inhabited by specialized exploiters of this rich supply of food. A third is the bulk of the water itself swarming with minute forms of life, both plant and animal, and known usually by the collective term plankton. If the pond is of more than average size, parts of its surface are

likely to be crowded with the leaves either of yellow water-lilies or of pondweed, possibly of both, and these anchorages of living green rafts will certainly support, during the warmer half of the year, a fauna richer perhaps than that of any other part of the pond – molluscs of several kinds, leeches, flatworms, the larvae of the chinamark moth, ensconced within dry pockets composed of leaf-fragments that they themselves have detached and shaped to their requirements, caddis-larvae in tubular cases, as well as great numbers of minute forms discernible only with lens or microscope. Yet another micro-habitat coming within the orbit of the pond is the mud at its edge, where buried head-downward in the mire and waving their tails so as to waft currents of oxygenated water towards them, are the ruddy-tinted colonies of tubifex worms.

There are times when a habitat is less easily defined, both as to its total extent and as to its parts. As an example I am thinking of one well known to me, a large sand-pit with perpendicular sides of yellow sand, variegated in places with those ripplings known to geologists as current-bedding. The pit is of glacial origin, the sand deposited there to a depth of fifty feet and more by the torrents that once poured from melting glaciers towards the end of the last Ice Age. During the summer the floor and the lower slopes are carpeted with the soft, round leaves of coltsfoot, and this is very much the dominant member of the plant community. The leaves, raised from six to twelve inches above ground-level, crowd together so as to form wide stretches of continuous canopy, a forest in miniature; and this arrangement divides the habitat into two well-defined parts, an upper and a lower, the upper one provided by the overlapping leaves of the coltsfoot, the lower roofed by their woolly undersides, thronged with their stems and floored by the sand of the pit. Here are two very different sub-habitats, the one exposed to sun and rain, the other sheltered, comparatively dry and encompassed by shadow. The corresponding animal communities are sharply distinguishable.

What might be called the lower storey, dry and sheltered, supports animals to which it is a permanent home, at least

during the summer. Clusters of greenfly (aphide) ensconce themselves snugly between the veins and the woolly tissue of the leaves, sucking perpetually at the sap. At least two kinds of small snail are commonly found and the coltsfoot leaves are their food. Less common than these are spiders, sometimes with their broods of spiderlings, woodlice, millipedes. Major predators such as wrens and blackbirds make an occasional visit to this pygmy forest. The upper storey of the crowded leaf-surfaces, on the other hand, supports an almost entirely different fauna, this time solely of insects – two-winged flies, hover-flies, ichneumons, craneflies, grasshoppers, ladybird beetles, and three or four different species of hunting wasp, the fly-hunters and the spider-hunters, to whom this is a productive hunting-ground. It is a community differing from the first in another respect, for its members are not permanent residents in the way that the others are. They are visitors, casuals, there for a particular purpose, and for the most part during the hours of sunshine only, rising at these times with a shrill buzz when disturbed. The surface of the leaf-canopy is not only a hunting-ground, but apparently a sort of promenade as well, and something too of a platform given over merely to basking in the sun. A degree of overlap is noticeable between the two communities. Ladybird beetles, found on the upper storey, certainly haunt the lower one as well. Some kinds of spider are found in both, and there is little doubt that some of the hunting wasps extend their deadly predation to the shade beneath the leaves.

So far there is relative simplicity where ub-divisions of the habitat are concerned. But what of the vertical or sharply sloping sides of the pit? Are they to be included within the general environment, or do they constitute a separate one? In more than one respect there is a close link between the two. The hunting wasps, for instance, make use of the bare sand-precipices to dig their burrows which they stock with paralysed flies as food for their larvae. One of them, *Mellinus arvensis*, a neat black and yellow wasp, is very common both here and in the hunting-ground of the coltsfoot leaves. Again, the sides of the pit are honeycombed with the holes of sand-martins, and

and these hawk freely through the air many feet above the coltsfoot-forest.

Boundaries of the habitat

We have arrived at the conception of the habitat and of the communities, both plant and animal, characteristic of it, of these as making up the basic ecological unit of life. We have seen that habitats differ enormously both as to their components and as to their size, and that their animal inhabitants are all ultimately dependent on the plant inhabitants. A further point is that animals are subject to a varying degree of overlap with regard to plant communities, this corresponding roughly to their size and mobility. But in spite of this, the limitations imposed on an animal community are sufficiently marked for it to be recognizable as such, which means that there must be certain barriers, limiting factors, to prevent unrestricted movement. Clearly the conditions that together make up a habitat – moisture, oxygen-content, temperature, and the rest – are those that the animal in question finds suitable. It is able to discover those conditions for itself to a large extent in a negative way because its physiological and nervous constitution enable it to respond unfavourably to conditions that would prove hostile. Marine animals, for instance, whose constitution is adapted to water heavily charged with salts, will avoid water that is fresh, because if they fail to do so they will perish. Natural selection has seen to that during the long course of their evolution. The instinctive power of avoidance has been handed on to them by their ancestors. On the other hand a positive response may be made, ability may be manifested to seek out conditions not so much favourable as essential. A butterfly will respond positively to the scent given out by a certain plant in such a way that she seeks out that plant and no other on which to lay her eggs. That too is determined by natural selection, since if the eggs are laid on the wrong plant the larvae will perish.

It by no means follows from this that a marked change in

any of the conditions making up a habitat will necessarily prove disastrous. Amongst them there is usually one, and perhaps only one, that must be maintained in a constant condition, and that will be the limiting factor. An animal may well be tolerant of changes of various sorts in its environment, and indeed this must be so considering that no environment remains constant for any great length of time. But if the limiting factor changes to a marked extent the result is certain to be disastrous to all animals limited by that factor. If a river changes its course and discharges volumes of fresh water into the sea at a different part of the coast, large numbers of marine animals are bound to perish. If some disease wipes out the one essential food-plant in a district at least one insect will become extinct. This will hold good everywhere, unless, as in fact frequently happens, the animal in question is capable of migrating from the affected environment to a similar one that has remained immune.

Now of all the factors that make up an environment it is not always easy to hit upon the limiting factor. An ecologist investigating the distribution of molluscs in a number of lakes might find that the temperature of the water differed markedly from one lake to another, and might well conclude that this was the reason for unevenness in distribution. He might overlook the fact that the lakes showed also a marked variation in the amount of lime held in solution, and that this was the cause he was looking for, since without lime the molluscs would be unable to clothe themselves with shells.

4

STRANDS OF DEPENDENCE: I

THE LAW OF THE JUNGLE

When we reflect on this struggle we may console ourselves with the full belief that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy and the happy survive and multiply

CHARLES DARWIN. *The Origin of Species*

TOWARDS the end of the last century the republic of Peru awoke to the fact that there was to be found on certain offshore islands along their coast a source of natural wealth of the greatest value. The Peruvians could and did make use of it themselves, but what was of far greater importance for them, they found that other nations also realized its value and were anxious to buy it in enormous quantities and at a fantastic profit to the exchequer of Peru. It appeared to be inexhaustible and consisted of a compact powdery substance which was simply excrement, the droppings of sea-birds, nesting there by the million, accumulated over the centuries and preserved in the rainless climate of those islands. They called it guano, a fertilizer of remarkable potency, and it meant so much to Peru that from the proceeds of its sale there arose public buildings in their cities, bridges over their rivers, warehouses, and docks for their ports, all, so to speak, founded on excrement. For some years it became possible to remit taxation, so enormous was the national revenue. Two things put an end to this golden age. One was the realization that the supply was by no means inexhaustible, that on many of the islands the spades of the excavators were gritting on the native rock. The other was the use of synthetic fertilizers. Today Peruvian guano is no longer an important export, although it is still extensively used in the irrigated fields of the coastal desert.

That is a story having human associations, and the economic aspect is of little interest to the ecologist, but the reasons for the existence of all those millions of tons of accumulated bird-droppings are of the utmost interest, for it is an example of a principle of the first importance in ecology. Investigating these reasons, we come upon a long and complicated chain of causation of which one end is represented by the ships of many nations stuffing their holds with ton after ton of natural fertilizer, and the other by an ocean current. This is the Humboldt or Peruvian Current flowing northwards from Antarctic waters for more than half the length of the South American continent, from Southern Chile to that point off the coast of Peru where it sweeps outwards in a great curve into the Pacific, driven by the South-east Trades. Because of its far southern origin the water of the current is several degrees colder than that through which it flows. Added to this, yet more cold water wells up from the depths to take the place of the surface-waters which are continuously displaced.

Now cold water is richer than warm in those chemical nitrates and phosphates on which plant-life in the sea, as elsewhere, depends. Polar seas are known to be richer in these substances than those nearer the equator. That is one reason why the northward-sweeping Humboldt Current is particularly rich in nitrates and phosphates. An additional reason is provided by those upwellings from the depths. Marine organisms, when they die, sink to the ocean floor and accumulate in deep drifts to form a great reservoir of these essential salts, with the result that upwellings of bottom-water are by comparison heavily charged with these same salts, causing the surface-water to be correspondingly rich. On this continuously renewed supply of vital salts an enormous wealth of marine plants (diatoms) flourishes exceedingly, providing an almost inexhaustible supply of food for rather larger but still minute animals. The minute animals in their turn provide food for fish, while the fish perform the same service for sea-birds.

It is this chain of cause and effect that accounts for the teeming life of the Bird Islands of Peru, one of the wonders of the

world – cormorants, boobies, pelicans in such numbers that they can be seen from the deck of a ship flying past at roosting-time in long wavering processions for hour after hour; or massed over shoals of fish and diving to prey upon them densely, blindingly, like snowflakes during a blizzard; roosting and nesting on the rocky offshore islands literally by the million. It is they who are the geese that lay the golden eggs of the guano. But something else must be taken into account, for without it their droppings would be found only in the form of white splashes on the rocks, instead of as deep dry deposits many feet thick. Those islands and the whole of this part of the coast of Peru enjoy (and for once this is surely the word) a climate in which rain is almost unknown. That too is a part of the pattern, intimately bound up with the cold current sweeping along the coast, and with the direction of the prevailing winds.

The whole thing is a chain, with the deposits of guano at one end and the current, with its nitrates and phosphates, at the other. This particular example has acquired fame because of its sensational economic importance, but for all that it is no more than an instance of a phenomenon of incalculable antiquity and world-wide occurrence wherever there is life. It is merely one example of a principle governing living creatures everywhere, in the sea, in fresh water, in deserts, in forests, in grasslands, in every kind of animal community. For the Humboldt Current is a habitat for life, supports a community of plants, in this instance of diatoms, which provides the biological foundation for an animal community of unbelievable complexity.

The principle of dependence

What is the primary distinction between an assemblage of living things, whether human or non-human, deserving to be called a society, and one which is undeserving of that title? The answer surely is dependence in some form or other, dependence of each member on the other members, and the community as a whole. Absence of dependence means each for himself and that is anarchy, the law of the jungle. Introduce dependence and

you introduce the beginnings of society, the rudiments of civilization. That is true of human communities: it is true also of those composed of animals. Animal communities are organized on a basis of dependence, and to say of them that they are governed by the law of the jungle, when by that we mean that they are not governed at all, is libellous and untrue. Obviously it would be absurd to draw a parallel between human and animal communities to any but a very limited extent, and the question arises: to what extent? It can be drawn further than to say that dependence is to be found in both. It can be drawn as far as to say that in both kinds of community two sorts of dependence are to be found, two sorts that are, or appear to be, in conflict with one another. We can call one of them competitive and the other cooperative dependence. Human beings compete with one another, but they cooperate as well. The same is true of animals.

The reasons for the existence of Peruvian guano given at the beginning of this chapter are an example of competitive dependence. The ecologist calls it a food-chain, and the dependence on which it is based is that of the predator on its prey. Without its prey the predator would starve. But dependence in nature is mutual more often than not. Can we trace mutualism here? Is it possible, without stretching a point beyond reasonable limits, to make out that the prey is dependent on the predator? Beyond question it is possible, provided we remember that what matters in the world of animals is the species rather than the individual. Without the predator to restrict its numbers within the limits of the resources of the environment, the prey would multiply so as to outrun its food-supply. Without the predator in fact the prey runs the risk of suffering the same fate as the predator deprived of its prey. It would starve.

The food-chain then is a part, and a highly important part, of the great web that binds all forms of life together, one of the more significant examples of that principle that life nowhere exists haphazardly, nowhere takes the form of an uncoordinated assemblage of predator and prey, but is organized,

graded to form a society in which there is fierce competition beyond question, but at the same time a sharing, a network of give and take, of exploiting and contributing. The food-chain is an example of competitive dependence, and in it we see at work that relentless struggle for existence, in which only the fit survive, that has so exercised the minds of inquirers since the time of Darwin. Tennyson summed it up in a phrase that has become proverbial, 'nature red in tooth and claw', and the apparent ferocity of it appalled him, as it has appalled so many. We are too apt to see it as a way of life in which the negation of law is turned into a principle, the law of the jungle, where only might is right. What we fail to realize is that this is no more than one form of dependence; that there are other forms deserving to be called cooperative. Modern ecology in no way denies the existence of fierce competition. Who that has seen a lion springing on to an antelope and tearing it to pieces, a peregrine swooping upon a pigeon, or a hunting wasp dragging a paralysed spider to her nest-hole, there to lay her egg on the spider's inert body so that the larva can devour it alive when it hatches from the egg, could deny that competition is relentless and widespread? What ecology has made clear is first that this remorseless competition is itself organized and graded; secondly that while the competitive form of dependence beyond question exists, there are other forms based on tolerance and cooperation. In this book the competitive forms will be examined first. The cooperative forms will be the subject of a separate chapter.

FOOD-CHAINS. Obviously food-chains will differ enormously from one animal community to another, but it is of the first importance to realize that all of them have certain features in common. The first is that without exception they are based on plants of one kind or another; that plants form the first link, diatoms in the sea and in fresh water, leaves of tree and herb in forest, grassland, and desert. This, of course, arises from the fact already stressed that animals cannot exist without plants. The green plant is the first link and the second is a species of

animal that feeds on the green plant. The third, fourth, and fifth, if there are as many as that in the chain, are other animals feeding on one another. These are carnivores, but since they all depend basically on a plant-eater, they too are to that extent herbivores, though at two or three removes. Each link in the chain then subsists on the one below, until the last is reached, the far end of the chain in the form of an animal having, as we say, no natural enemies. Each chain is comparatively simple, made up of not more than four or five links, on occasions only two. But this is as far as possible from saying that simplicity governs the system as a whole. On the contrary there is extreme complexity in the relationship of chains to one another, in the entire food-cycle of any given animal community. It is in the animal community as a whole that we find the close-knit, criss-crossing web of competitive dependence.

SIZE AND NUMBER. A second important principle is concerned with the size of animals and their numbers in the separate links. In nature there is a general rule that the prey of an animal is smaller than itself. For this reason, as the chain is traced upwards from its plant foundation, the animals composing the links become progressively larger. The animal forming the last link is the largest of them all. That is a relationship of size, but there is one also of numbers, and the two are bound up so that the double relationship can be expressed in one sentence, to the effect that the smaller the animal the greater its numbers. This means that as the chain is traced upwards, we find a large number of small creatures being preyed upon by a smaller number of larger creatures. The idea could be expressed graphically as a pyramid with a broad base representing, say, the uncountable leaves of a forest. As the sides of the pyramid begin to converge we come upon aphids or greenfly feeding on the leaves. After that, still climbing the pyramid, we find beetles larger than the aphids but less numerous, using them as food. Then come birds, such as tits and warblers, feeding on the beetles. Last of all there is the apex of the pyramid

represented perhaps by a single pair of sparrow-hawks preying on the small birds, but without a natural enemy of their own, unless we include the gamekeeper with his gun. But the gamekeeper is a complication of another sort. Far better for my purpose to leave the apex of the pyramid in possession of the pair of sparrow-hawks.

The pyramid is in many ways a more useful figure of speech than the chain, since while emphasizing the idea of dependent links or steps, it includes also that of diminishing numbers. It will be as well to make sure that its biological foundations are secure. These are twofold, concerned with two assumptions. Are they sound assumptions? The first is to the effect that animals tend to prey on creatures smaller than themselves. That this can be accepted with little demur is, in fact, to a large extent a matter of common sense. No animal will find it worth while attacking another animal larger than itself, unless like a poisonous or constricting snake it has a special device enabling it to do so. But there is a lower as well as an upper limit. It would be no less a waste of time and energy to seek out prey so small as to be incapable of satisfying its needs. True, if the animal caught and devoured a sufficient number of very small creatures its needs would be satisfied in time. But the time required would be too long. Far better to seek out larger creatures. The prey of an animal, therefore, must be neither too large nor too small.

But exceptions are sometimes helpful and often interesting, and just as in the case of the poisonous snake in connexion with the upper limit of size, so there is an exception of this kind in connexion with the lower limit. There are certain kinds of whale, the baleen- or whalebone-whales, that have found it abundantly worth while to subsist on enormous numbers of a creature smaller than themselves by many thousands of parts. The baleen-whales live by engulfing a sort of thick soup composed of sea water containing prodigious quantities of minute shrimp-like animals collectively known as krill. The water is strained out through the whalebone sieve. So here is another specialized structural modification, and it is clear that one or

more links in the normal food-chain of marine animals have been by-passed. It is as though some remarkable hawk had acquired the skill to gorge itself on immense numbers of aphids. It can be added here that this by-passing of links occurs also in an English woodland. Small birds quite frequently feed directly on aphids.

The other foundation of the pyramid is concerned with numbers. Why is its base the broadest part? What is it that prevents the aphids, preyed upon directly or indirectly by so many woodland animals, from being exterminated? Why is it that our one pair of sparrow-hawks, so happily free from enemies, do not for that reason multiply so that the wood becomes murmurous with their wings? The answer is that broadly speaking the smaller the creature the greater its rate of reproduction. Most gardeners are only too well aware of the fantastic rate of reproduction of aphids. So concerned are these insects with propagating their kind that for most of the summer they dispense with the sexual process altogether and increase by virgin-birth or parthenogenesis, no males taking part. The larvae of hover-flies and both the larvae and adults of ladybird beetles, prolific enough, are less so than the aphids. So it goes on up to the sparrow-hawks, producing at the most four or five young in a season. This principle can be accepted as being true in the broadest sense and for the ecologist's purpose it needs to be true in that sense only. Most certainly there are exceptions, but they are not enough to offset the effectiveness of the principle.

NICHES. Intimately bound up with the food-chain or the pyramid of numbers is another and equally important principle governing all animal communities, and here too a parallel with human societies suggests itself. There are many ways of distinguishing human beings from one another, but the one we find most convenient is by means of their occupations, by the way they earn their living. The same applies to animals and this is the method used by the ecologist who distinguishes animals by the way they earn their living, by the kind of food

that is their staple. It is this that determines the place, the ecological niche, of an animal in its community.

In the broadest sense we can place an animal in one of three niches, the herbivore, the carnivore and the scavenger. But the ecologist goes further. Each of these, particularly perhaps the second, can be divided according to more or less specialized feeding habits. In a wood for example there is the aphid-eating niche occupied by certain beetles and by the larvae of some of the hover-flies. This is a highly important niche in any wood. In the sea there is a correspondingly important one filled by small crustaceans known as copepods which feed directly upon diatoms. By so doing and because of their great numbers and wide distribution, they are themselves the food for many kinds of fish. The copepods occupy so useful a niche in the marine community that the expressive term 'key-industry' was applied to them and to others like them by the very eminent ecologist Dr Charles Elton. There are many other kinds of niche. Carnivores can be divided, for instance, into those that live on small mammals, such as mice and shrews, on the one hand, and into those that live on insects on the other. It is possible to split up insectivores into those specializing in certain varieties of insect diet.

Every species of animal then in a community has its niche. It is here that restriction of competition comes into play, for the niche system acts so as to cut down competition to a minimum. Even when there are different species in a community depending on the same food, there are means for keeping them apart. Insectivorous birds, for instance, tend to use different parts of a habitat, even different parts of the same tree, in their search for food. Sometimes two species requiring the same food are kept apart because one is diurnal in its habits, while the other is nocturnal. The nocturnal counterpart of the sparrow-hawk is the tawny owl. In many communities there are various insects that are pollen-feeders. Among them competition is restricted by the fact that they reach the adult stage at different times of the year, when the plants upon which they depend are in flower.

A point worth keeping in mind is that similar sorts of niche are often found in widely dissimilar kinds of animal community. These communities may be adjoining ones in a country such as Britain, where in a woodland community a mouse-eating niche may be filled by tawny owls, while in the fields outside another mouse-eating niche is filled by kestrels. The communities on the other hand may be widely separated. Dr Elton in *Animal Ecology* quotes examples of a niche filled by birds that habitually hunt for ticks on the backs of large mammals. Examples of this specialized occupation are found in tropical Africa, where the tick-bird spends its time on the backs of antelopes and buffaloes. In England a similar niche on sheep is filled by starlings. Sometimes the niche includes breeding habits as well as food. In England, for instance, sand-martins nest in cliffs of sand and hawk for insects over the surface of ponds. Bee-eaters in the Nile Valley live in very much the same way.

TERRITORIES. There is another aspect of competitive dependence which at first sight looks like competition, not for food so much as for living-space. But since living-space is important to an animal because of the food to be found within it as well as for purposes of sheer elbow-room, this aspect too must be related, partly at least, to the paramount necessity for getting enough to eat. The fact is that very many of the higher animals have a strongly developed territorial instinct. That is to say they mark out a territory for themselves which they are prepared to defend, not only against other species but more particularly against their own kind. The instinct is made use of by many fishes, almost all birds, and many kinds of mammal, but it is birds that have received the greater share of attention since Eliot Howard, in the twenties, first made the principle known. There is no doubt that this system of territories is immensely important in the lives of a great many species of animal, and this in more than one way.

In essence it is simple enough. The world is crowded with living things, so much so that space on occasions is limited.

For this reason there is nothing surprising in the fact that many animals, at any rate for part of the year, should exercise landlord rights over a portion of the earth's surface which for the time being becomes an estate where trespassers will be prosecuted to the extent of being attacked or at any rate threatened by a hostile display. Fundamentally this is a matter of restricting, of organizing, what would otherwise be anarchy. But anarchy is already restricted by means of the food-chain, coupled with the system of niches. It seems, therefore, that these are not enough, that a further restriction is called for, and this is provided by the marking out of territories. Can we find any need for this additional restriction? We can if we remember that there is a season in the annual life-cycle of an animal when a sufficient supply of food becomes particularly urgent, and that is during the breeding season, when a mated pair has to find food not only for itself but for the young as well. At that time the demands made by an animal on the food-resources of its habitat may become extreme. Hence the territory, hence the intimate, and it might well appear, exclusive connexion between the territory and the breeding season.

But territories are known to have a direct bearing on phases of the life-cycle other than the feeding of a brood. They have a direct bearing on courtship, on rivalry between males, on the finding of a mate, on the colours and aggressive displays of male animals, the song of birds, and the frequent contrast between the liveries of male and female. The territory, therefore, is a phenomenon of some complexity, and it is not surprising that there should be disagreement among ecologists as to its full significance. The various points can be made clear by examples treated in detail.

For the greater part of the year three-spined sticklebacks in a pond cruise about with apparent vagueness, companionably in small shoals, males and females together. During this period also, lasting from July to about the end of March, there is little outward distinction between the sexes. At about the beginning of April a marked change takes place. Indeterminate cruising disappears, the companionship and tolerance of the shoal

give way to a totally different set of conditions. The males show a desire for solitude, and at the same time begin to take on striking habiliments, a breast of glowing ruby red, a suffusion of electric blue over the greater part of the body. The eyes, also of a milky blue, become more prominent. These are their nuptial colours, their wedding garments, and with them they acquire a pugnacious temper, so that the spring coloration is associated not only with mating, but with a fierce intolerance towards members of their own species. They are in fighting trim.

But the all-important point is that this is not a matter of solitude and aggressiveness anywhere, but in one particular spot only, for all these changes are bound up in intimate relationship with a circumscribed cubic foot or so of water, weed and muddy floor, over which the male stickleback proclaims his lordship with every means at his disposal. His movements, leisurely heretofore, become vigorous and swift. He swims back and forth in flashing curves, punctuated with intervals of immobility, when as it were he treads water with flickering fins. He flaunts his gay colours to maximum effect. He grimaces defiance by opening and shutting his mouth. He may erect his dorsal spines like standards, but above all he chases from his territory any trespassing males. These other males, all in the same condition, will have marked out territories of their own, and it is where adjoining territories meet that the peace of the pond is most frequently broken. Border demonstrations, frontier forays, occur continually. On occasions one male will chase another deep into enemy territory, but always he returns at once to the security of his own domain. For nearly all of this is bluff, a matter of threat and counter-threat. Actual combat in the sense of the infliction of injury is very rare, and each male stickleback is swayed by two conflicting urges, the urge to attack and the urge to retreat.

Defence of his territory is far from being his only activity. The all-important urge towards reproduction is equally strong. This he expresses by building a nest somewhere near the centre of the territory, a mass of weed collected piece by piece with the same tireless energy typical of all his activities at this time. The

nest grows steadily, and the builder, depending on his own unassisted efforts, cements it together with a glutinous secretion from his kidneys. This done to his satisfaction, he bores his way through the midst of it, converting it into a tunnel.

This nest-building is punctuated by intervals of chasing, not males only but inquisitive females as well. But sooner or later one of the females, her abdomen already swollen with developing eggs, will respond to his intimidating advances by taking up a submissive posture, head up towards the male in such a way as to bring to his notice her swollen belly. Then a fresh phase begins. The male darts to the nest and the female follows. He enters with the object of showing her what she is expected to do, and perhaps after one or two abortive attempts, she insinuates herself into the tunnel to perform that essential act which is her solitary contribution to this complex chain of events. Even in this she needs his assistance, and he hovers above, prodding the base of her tail as encouragement and stimulus. When the eggs have been laid it is for the male once more to enter the nest, this time to fertilize them. But that is very far from being the last of his onerous duties. In fact it is now that the most exacting phase begins, for the eggs call for unremitting attention, not in the way of their defence, though that necessity exists and is attended to, but in the way of their aeration. The eggs, if they are to hatch, require oxygen in quantities greater than they could find simply by lying in the nest. It is the business of the male to provide it, and he does so by taking up a position above them and winnowing the water with his fins so that fresh currents are directed over them.

After many days of assiduous attention, the eggs hatch and then the tiny fry have to be guarded from predators, have to be carefully shepherded, so that some among them will not show more exploratory enterprise than is good for them at this tender age. After a while they can fend for themselves, and the devoted father who has done everything for them except the one thing he is physically incapable of doing, namely start them off in life as eggs, is at last free to spend the rest of the year in comparative leisure. His colours quickly fade and he

swims away, abandoning his territory which has served its purpose and as such ceases to exist.

The breeding cycle of the three-spined stickleback has been described in detail because it so beautifully exemplifies the territory principle, and because it has been intensively studied. Many more details could have been added, all of them of fascinating interest, all in some degree bound up with the territory, but belonging perhaps more strictly to the study of animal behaviour. They will receive attention later. The territory system, of very wide occurrence among vertebrates, and exemplified among fishes other than the stickleback, is traceable perhaps among some molluscs, as well as among a few of the insects. There is, for instance, a dragonfly, the green demoiselle (*Agrion virgo*), of which the male becomes fiercely intolerant of other males, chasing them vigorously from his own chosen perch, defending by so doing what looks very much like a territory. Little more than a beginning has been made where mammals are concerned, but many of them are known to mark out territories, defining their boundaries in some instances by depositing scent from specialized glands, in others by excretion. We are all familiar with the habits of dogs.

Among birds the close correspondence between territory and breeding is clearly shown, though there are some rather puzzling instances, for instance among robins, of the maintenance of territories for many months after the breeding season. But since the territory system is so widespread among birds, there is little reason for dealing in detail with one specific example. The risks inevitably attendant on the making of generalizations can with reasonable confidence be taken. The birds that breed here in Britain are either residents or spring migrants, and the territory system is well established with regard to both. Residents during the winter are fairly widely dispersed over the countryside, some gathered in flocks of more than one species, ranging woods and hedges for food, others migrating within circumscribed limits. The spring migrants at that time are somewhere far to the south, scattered over Southern Europe and the greater part of Africa. They

reach our shores at intervals according to species from the end of March to well into May.

In both these large groups, as soon as the urge to breed begins to assert itself, a marked change in behaviour takes place, and as with the stickleback, this is a matter of intolerance replacing tolerance, companionship giving way to solitude, a greater or less degree of nomadism becoming supplanted by aggressive attachment to a circumscribed patch of the earth's surface. On the one hand the foraging winter flocks of finches, buntings, and tits begin to break up; on the other, the hosts of small warblers, who have made their astonishing northward journeys together, drop down out of the sky. In both groups the males, initiating the cycle, soon begin to take up territories, begin too to make their voices heard: the chiffchaff with his chiff-chaff, the willow-warbler with his dying fall, and the nightingale with his song to tax the poetic genius of a Keats, and a score of others.

The song of birds means so much to us, bound up as it is with the gladness and the resurgence of hope that spring conveys, that we are much inclined to interpret it as an expression of that joy and hope. Who would take it upon himself to scoff at that interpretation? Not, I should hope, the open-minded ecologist, though he might well protest that such considerations are not his concern. What is his concern is to interpret the song of birds on the basis of observed facts, and these have taught him to give it at least a double significance. We now know, for instance, that the song of the nightingale, for all its legendary richness, is entirely practical, with two meanings in particular: on the one hand a proclamation of proprietary rights, a challenge and a keep-off sign to rivals, and on the other an invitation to a potential mate. On the whole it seems that the first, at least at the start, is of greater import than the second. Many birds go out of their way to make themselves conspicuous while singing, some like the blackbird and the song-thrush perching on the topmost branch of a tree. These perhaps are extreme examples, as is the skylark mounting his bright ladder of song, but most

birds make use of some sort of singing-post which becomes in a manner their headquarters within the territory. The sedge-warbler and the reed-warbler on the other hand seem to delight in singing from the heart of a thicket or reed-bed.

But this attitude towards those call-notes of birds that we find pleasing and so designate as song, as well as those harsher ones undeserving of the name, is not enough. It is too mechanistic, too much concerned with things external to the bird itself, conveying truth but not the whole truth. To arrive at the whole truth, or at any rate nearer to that goal, we could hardly do better than go back to the sentence at the beginning of the last paragraph, which conveyed the idea that the song of birds is an expression of joy and hope. If objection should be made that joy and hope are human and not avian emotions, let us call it zest for living. A bird sings because it wants to sing. In that simple statement surely there is a large measure of truth. Students of animal behaviour do not fail to acknowledge the fact, but are much inclined to reduce it to terms of hormones secreted by the endocrine glands, to a physiological condition confined to the breeding season. But song can be regarded as the outward expression of an urge present in varying degrees at all times. Many birds sing at times other than the breeding-season and in places other than the territory. Robins sing for the greater part of the year. So do skylarks. Thrushes begin singing in December.

How then are we to reconcile this more generalized view with the specific one that the purpose of song is to warn off a rival or to attract a mate? Obviously the reconciliation is of primary importance, and we can make it by believing that the generalized and inward urge has been, so to speak, seized upon by natural selection, given a specific purpose appropriate to certain times and certain places, when an intensification of song is of biological advantage to the species. In this way it has acquired survival value down the ages.

With regard to territories there is a clear parallel between birds and sticklebacks. The warbler perches conspicuously

and sings his heart away. The stickleback, denied the gift of song, flaunts his red breast and draws attention to himself by swimming strongly round his territory. Again, it is true that among many birds the cock wears gaudy plumage. As with the stickleback this has much to do with rivalry between males and with courtship; and birds, like sticklebacks, will defend their territories with the utmost determination against trespassers. A singing blackbird will break off his song when a rival appears in his territory, drop in a flash to the ground, and chase him away. Usually, once again it is a matter of bluff, but there are times when rival cocks will lock together in desperate and prolonged combat. But before long they separate, both to all appearances free from injury. This too we would expect, since the frequent infliction of injury would be a grievous disadvantage to the species.

It seems clear, at least in most instances, that posturing and fighting are carried out by cocks against other cocks considered as trespassers in the territory more than as rivals for the favours of the hen. The hen-bird may not appear on the scene at all at the beginning, or if she does gives every indication of complete indifference to the rivalry of the cocks. But in spite of this, she can scarcely be considered as anything but a highly important component of the pattern. Sooner or later the prospective mate appears in the territory attracted by the song of the cock, who frequently shows so little understanding of what her presence means that he will chase her away. There is no doubt that appeasement is a very necessary part of the process of courtship, and if the urge in the hen towards mating is stronger than her urge to retreat, she will indicate the fact by some specific and established gesture of submission, to which the cock sooner or later responds. There follows mating, nest-building, and the rearing of the brood, almost always within the confines of the territory.

This is the general pattern, while details will vary from species to species. Gregarious nesters, like gannets and rooks, can be thought of on the one hand as devoid of the territorial instinct, or on the other and perhaps more truthfully, as

having narrowed their territories to the immediate surroundings of each nest. If this is the correct view, the difference in the size of territories as between gregarious and solitary nesters is explained by the fact that in the former the amount of available food is not dependent on the size of the territory.

This leads to the problem of the significance of territories in the widest sense. That they must confer considerable biological advantage seems clear from their widespread occurrence. There can be no doubt that the system is closely adaptive to conditions within the animal community. Can we say precisely in what way? It happens that here, as often, it is not difficult to suggest reasons for their importance on theoretical grounds. Territories could be valuable in saving indiscriminate and severe fighting, and this is borne out by the way in which a trespassing cock, or male stickleback, will immediately retreat after invading the territory of a rival. He seems to know that he is on alien ground and that this means trouble. If it were not for the territory system, he would probably stand fast and a bitter fight would result. Secondly the territory could save time in the search for food. If an animal can regard a certain area as his within limits and use it as a more or less exclusive larder, much time and energy will be saved. This would be particularly important if there is a brood of exacting and delicate youngsters to keep both parents busy during the hours of daylight. In many species, these youngsters, are likely to die from exposure during their early stages if abandoned for long periods by parents ranging over a wide area for food. A third point is that the territory makes easier the finding of mates, and when this has been done, tightens the bond between male and female so that they are more likely to stay together. Finally, and in some ways most important of all, it could have a direct and controlling influence on the density of a species over a given area. If it could be shown that the size of the territory remains nearly the same for each species, that this specific size was intimately bound up with minimum food requirements both for parents and brood, then the system would exercise the most rigid

control over the number of nesting pairs of birds that a habitat is capable of accommodating.

Now the ecologist, or for that matter any scientific worker, soon finds that it is one thing to propound a theory that seems to fit the facts, that is tidy and satisfying; and frequently quite another to confirm his theory by means of experiments. After all it is evidence that counts. So it is with territories, and the fact is that controversy still rages round the subject. It can almost certainly be accepted that the system effects some degree of spacing out, but that territories are constant in size for each species and are intimately related to minimum food requirements are both denied by David Lack, whose opinion deserves respect, for he has carried out an exhaustive study of these matters, as well as most others, in the life of what is undoubtedly our favourite bird, the robin. He finds, for instance, that the territories of robins vary widely in size, and that they feed frequently outside the territory. We can probably believe that the territory system reduces fighting, that in many cases it saves time and energy in the search for food, particularly when there is a brood to feed, that it helps to bring animals of the same species together with a view to mating and tightens the bond between them, and finally that it effects a loose spacing out. That is as far as agreement goes, and after all it is a good deal.

Considering the system from the point of view, not of one species, but of several, of all territory-holding animals in any community, clearly the situation becomes highly complex. The size of a territory would vary directly with the size and mobility of the animal. That of a pair of golden eagles, for instance, might well cover a square mile or more. It might comprise the territories of several pairs, say, of greenshanks, while each of these in their turn would certainly include those of a number of pairs of meadow-pipits. This is comparatively simple. A map of the territories of all the nesting birds in a wood, to say nothing of those of other animals, would be almost impossible to decipher, even if it could ever be drawn.

Density

The connexion between territories and density brings me logically to the problem of density in general. We are concerned here as always, with an animal community of many species, each occupying its own niche, and each linked with all the others by means of the various food chains in a highly complex web of predator and prey. From this it follows that the density of any one species is a matter of the utmost importance, not only for the species concerned but for the others as well. Now it is probable that most people giving thought to such matters would conclude that the density of a species remains the same over long periods of time. They would refer to a vaguely understood law known as the balance of nature, supposing that this balance is maintained by natural checks on the rate of reproduction. They would be right up to a point. There are checks on the fecundity of animals. There must be, or the world would be overrun. All the same it is necessary to state here that the balance of nature, in this sense, is to a very large extent a myth. It is very much of a myth if by it we understand an unvarying density of animal populations. Numbers are far from being constant. They fluctuate continually, sometimes wildly, and in a number of instances with a strange regularity. This is a matter of the greatest importance in two distinct ways, first because of the influence of these fluctuations on other members of the community, second because they affect also the evolution of species.

The second of these considerations will be referred to in a later chapter. Something must now be said about the first. The important thing to keep in mind is the universal success of all animals in propagating their kind. It is, so to speak, an engine of such tremendous power that it has to be checked, and this is done to some extent by the system of food-chains, giving rise to a semblance of balance. But this is not enough. Disease, for instance, might thin the ranks of a predator

species so that its prey increases out of all proportion. This is only one of a number of possible influences, and these could be either external to the animals themselves, climatic for instance, or internal such as disease caused perhaps by an increase of parasites. Any of these factors could upset the balance in one direction or the other, and could make itself felt throughout the community. But the point to make here is that every species considered separately tends to increase towards maximum density, to reach a condition of over-crowding.

This is a dangerous state of affairs, since food supply is bound to be threatened, and the incidence of disease and of parasite-infestation will increase in direct proportion to pressure of numbers. But in spite of this tendency on the part of every species to increase, there are occasions in an animal community when one species or another diminishes in numbers. There may be climatic reasons for a downward swing, or reasons internal to the species or to the community. This too has its dangers, some of which may be obvious enough. Density may become so low that the sexes find difficulty in meeting. Quite apart from such obvious dangers, it is now known that there are others It has been proved experimentally, for instance, that the length of life of the fruit-fly, *Drosophila*, becomes reduced when the population sinks below a certain level. There is evidence also for the belief that their rate of reproduction is apt to be slowed down in the same circumstances.

To approach an understanding of this rather difficult matter we must think of the animal community as something dynamic, as subjected continuously to varied stresses and strains, both external and internal. These stresses and strains, or one of them in particular, may act at one time so as to favour the natural rate of increase of a species, at another so as to oppose it. The result is a series of oscillations, upswings and down-swings, both of them tending to bring about a dangerous state of affairs if carried to extremes. The desirable state of affairs is neither the one nor the other, but something inter-

mediate between the two, an optimum density as it is called. This optimum density becomes a sort of goal towards which every species strives, not by its own efforts but as a result of the stresses and strains to which the whole community is subjected. Because of the extreme complexity of all the component parts of a community, the optimum density is seldom reached by any one species, and its numbers oscillate above and below the optimum. For the most part these oscillations are moderate in extent, normal and familiar. In one year, for instance, there are distinctly more, or distinctly fewer, wasps than in the next. Examples of immoderate, less frequent, and sometimes staggering oscillations are those plagues of locusts, of caterpillars, or of mice that have often been recorded.

Obviously the effect of fluctuations of both kinds on the other members of the community are various and widespread. The greater they are the deeper and the wider the effects. Some of them have been intensively studied because of their economic importance. For instance, it has become clear from the records of the number of furs brought in over a period of years to the Hudson Bay Company in Northern Canada that all the fur-bearing animals of this great region of coniferous forest and tundra are subject to those wide and strangely regular fluctuations previously mentioned. The one exception seems to be the beaver. Two things are particularly interesting about these fluctuations. One is their regularity, and the other the way in which years of boom and slump often correspond when more than one species is being considered. For instance, the snowshoe rabbit, the lynx, and the red fox fluctuate in cycles of eleven years, that is to say, a period of eleven years separates one boom from the next. The arctic fox, on the other hand, fluctuates according to a three-year cycle.

The cause of the regularity is unknown, but correspondence of increase between one animal and another is clearly dependent on the fact that one feeds on the other, increasing when it is abundant. In Northern Labrador, for instance, there

was a plague of mice in the year 1905, and this caused an increase in the numbers of foxes, of owls, and of hawks. The increase of mice reached plague dimensions, but, because of their slower rate of increase, this was not true of the foxes and the birds. On occasions such as this the lag in the increase of the predator animals can be so marked that they make little impression on the swarming prey. In Nevada a mouse-plague occurred in 1907, when thousands of acres of clover were destroyed and the ground over square miles of country was closely perforated with their holes. At the same time thousands of birds of prey and carnivorous mammals were feasting royally on the mice to the tune of a million or so every month, without appreciable effect on their numbers.

Now these of course are recorded effects, recorded because of their economic importance. There would be many others penetrating right through the animal communities concerned; but these others, effects on the smaller birds, on insects, on parasites and scavengers, might be equally great, though unnoticed and unrecorded.

It seems that every animal community may be, and from time to time is, subject to fluctuations of this kind, and the question suggests itself: do communities differ from one another in being more or less subject? At least a tentative answer can be given. It seems probable that it is a matter of the relative constancy of an environment. Most land habitats are subject to changing conditions, changes not seasonal so much as occurring at intervals of years. The Canadian Arctic is certainly one of these. On the other hand, as I have already pointed out, there are two major habitats far less subject to change. One is the equatorial forest, and the other the great oceanic basins. In these two, we may reasonably suppose, wide fluctuations in the numbers of animals are less likely to occur.

Parasitism

There remains one other form of competitive dependence, one that is exceedingly important, and from the human point of view exceedingly unattractive, far more so than any other.

Most of us feel that though the relationship between predator and prey is savage and relentless, it is something we can accept, if for no other reason than that we practise it ourselves. That between parasite and host, on the other hand, we regard as repulsive, far less easily acceptable to fastidious minds than any other of nature's ways. This is an understandable prejudice, but like all prejudices basically illogical. We are deeply moved by the beauty of living creatures. This beauty takes many forms, the most noticeable being of colour and shape. Another and almost equally important is that of adaptation to circumstances of their lives. The bumble-bee exploring the flowers of a foxglove spire, a swift cleaving the air with a scimitar of black wings, the Indian leaf butterfly, with the underside of its wings counterfeiting a leaf not only in shape, but in markings as well; all these and hundreds of others are miracles of adaptation and are beautiful for precisely that reason. But what could be more of a miracle of adaptation than a tapeworm which has degenerated to little more than a set of hooks and a series of detachable segments, each containing eggs by the thousand. Sightless, immobile, living in total darkness and bathed perpetually in its food which it absorbs through the skin, it has no need for any of the attributes it has forsworn. Alternatively consider the swift mentioned above. This bird, and particularly the nestling, is infested with anything up to twelve louse-flies, flightless, blood-sucking, and of repulsive aspect, each one as big in proportion to its host as a moderate-size crab would be to a human body. The louse-fly produces a single larva which pupates at once and survives the winter in or near the nest. From this pupa an adult emerges, timing its emergence with the hatching of the swift's eggs in June. Adaptation could scarcely go further.

There is another point of view which should make us hesitate to accuse parasites of degenerate, still less of reprehensible, behaviour. To do so is to regard the natural world from a purely human standpoint. Who are we to pass judgement? It is of course true that there is a big difference between

an animal that devours another and one that lives on or in a permanent host; and this difference, as Charles Elton has vividly pointed out, is that between living on capital, which is the way of the carnivore, and living on income, which is the way of the parasite. Foxes eat rabbits, and in so doing destroy them so that they are no longer capable of providing food; but the tapeworm inhabiting a rabbit goes one better and induces the rabbit to supply it with sustenance for as long as the rabbit continues to live. The resemblance is really more important than the difference, and this is made clearer still by the fact that, as so often in nature, there is no sharply dividing line between the one way of life and the other. The tapeworm is a confirmed and dedicated parasite, its host the rabbit a free-living creature. But in between these extremes there are many connecting links. The louse, like the tapeworm, is a parasite but less completely so, since it will remove itself from one host to another. The flea goes further and spends much of its time wandering abroad. The warble-fly is a parasite for its larval stage only, while as for the blood-sucking flies, it is not easy to say whether they are carnivores or parasites.

Parasitism, whether we like it or not, is a widespread and highly successful way of life. It is a way of life moreover subject to rules and restrictions like any other. Complete parasites, that is to say those that pass the whole or the major part of their lives on or in their host, have a really remarkable achievement to their credit, for while they are predators they have succeeded in converting their prey into their environment. With them habitat and food are one and the same. It is for this reason, if for no other, that they are very much the concern of the ecologist. As for the general success of parasites, we have only to consider that for instance a bird, almost any kind of bird, is quite likely to harbour some twenty different kinds of parasite in all parts of its body, internally and externally – protozoa and bacteria in the blood-stream; worms of various kinds, flukes, tapeworms, round-worms, leeches, in the digestive system, in the bronchial

tubes, in the air-sacs and lungs; bugs, fleas, feather-lice, mites and ticks, infesting the plumage and the skin. The number of parasites of one kind or another is sometimes past belief. Over ten thousand nematode worms, for instance, have been taken from a single grouse.

Some parasites, such as many of the feather-lice of birds, are host-specific, which means that they infest one kind of bird and one only. So frequently does this happen that they have been made use of to trace the descent of certain closely related species of bird. As a way of living, parasitism varies in the closeness of physical intimacy between parasitic associations of two free-living animals at one extreme, and actual physiological union at the other. Of the first group there are several examples. One is the pirate or klepto-parasite, such as the skua that harries gulls until they disgorge the fish they have swallowed. Then there is the brood-parasite like our familiar cuckoo whose evasion of parental responsibilities is well known, or the ichneumon fly that lays her eggs in the living bodies of certain caterpillars. There are parasitoids like the hunting wasps to whom the host is a fly or a spider which serves as food for the larvae of the wasp. Of the second group, involving the most intimate forms of parasitism, perhaps the strangest example is found in some of the deep-sea angler fish among whom parasitism is a matter of sex. The depths of the sea constitute an environment so enormous as to be sparsely settled. This means that, especially with rather lethargic lurkers like these angler fish, it is no easy matter for male and female to meet. Once met it is advisable never to part. The male, the more active of the two, is little more than a quarter as big as the female. He probably tracks her down by some chemical means, and having found her attaches himself in so intimate a manner that the blood-streams of the two actually unite.

What are the rules of the parasite game? There is one golden one, to work out a compromise between drawing all possible sustenance from the host on the one hand, and on the other grievously impairing or even killing it in the process.

The flow of income must be at once adequate and perennial while life endures. Are the odds entirely against the host? It is true that as a rule it seems to come to no permanent harm, and can hit back to some slight extent by preening, dust-bathing, scratching or biting, but such measures are of use only against ecto-parasites (those parasites that live on the outside of the host). There is little that the host can do against the sheltered endo-parasite, except tolerate it.

PARASITISM AND ECOLOGY. Since, as I have said, to the parasite its host is also its habitat, there is no aspect of the subject that can fail to be of interest to the ecologist. There are two above all that are his concern. One is the response of the parasite to its environment, in other words the adaptations consequent upon so specialized a mode of life. To study these is indeed to enter a bizarre world.

In the first place it must be understood that parasitism offers a secure and comfortable existence once it has been established. It would hardly be possible to over-emphasize the weightiness of the qualification in that sentence for, as though to exact payment for easy living, the road leading to the desired goal is frequently obstructed with unbelievable hazards. Outstanding among these is the mathematical improbability of the larvae ever finding the right host. Consider for instance the round-worm that infests grouse. The eggs are scattered over the heather-covered hills, and when they hatch the larvae crawl to the tips of the heather-shoots, which are the food of the grouse. If one of these harbouring a round-worm larva is eaten by one of the birds, all is well from the point of view of the parasite. If this does not happen the larva perishes The odds against any of them must be of the order of millions to one.

The same sort of astronomical mortality must apply to ticks in tropical grasslands and leeches in the equatorial forest. As a result parasites generally possess a correspondingly astronomical fertility. They must lay eggs on an enormous scale and their reproductive organs must develop in order to

do so. But that is not enough, and we find among parasites, as nowhere else to the same extent, a number of highly specialized reproductive devices. Consider first the problem of those in which the sexes are in different individuals, which means that two must enter the body of the host and these two of opposite sexes. The odds are heavy against them, and there are further heavy odds against the two meeting. To do so is a triumph and the most must be made of it. As with the angler fish already referred to, they must never be allowed to separate, and so in one kind of fluke for instance the male embeds the female in a groove in its side; and this condition, approximating to that of a parasite on a parasite, prevails until the eggs are fertilized. Parthenogenesis, or virgin-birth, is a practice fully recognized, to such effect indeed that among some of the nematodes or round-worms no males have ever been found. On occasions non-sexual forms of reproduction are added to sexual ones. Thus the fertilized egg of a trematode or fluke may split up within the body of its intermediate host into several million larvae. Some tapeworms multiply simply by budding in the larval stage, or by giving off chains of individuals when adult.

Quite apart from these reproductive adaptations are certain characteristic structural ones. This is largely a matter of atrophy, of dispensing with parts of the body for which a parasite has no use. Limbs were among the first to go. All that many of them need are hooks or spines for hanging on. Consequently feather-lice, bugs, and fleas have either lost their wings, or retain them only as useless vestiges, while their mouth-parts are equipped with spines, often recurved. Leeches have suckers and exude a saliva which prevents coagulation of the blood of their victim. Many parasites have no need for either mouth-parts or a digestive tract, since nutriment is absorbed through the surface of the body. Eyes and ears are equally unnecessary for liver-flukes or feather-mites which have instead a specialized sense or tropism to guide them unerringly to the required part of the host's body.

LIFE-CYCLES. It must be remembered that parasites, having, as I have said, converted their food-supply into their environment, are in fact closely bound up with two environments, that of their host's body and that much wider one to which the host belongs. Feather-lice and mites pass successive generations on the same victim, and are not called upon to face the hazards of the outside world. Most parasites are less fortunate, having larval stages, when for a time they must fend for themselves and become free-living creatures in a hostile world. As soon as they are eaten by the appropriate animal their parasitic adult stage begins. Here then is a relationship with the habitat of the outer scene, and perhaps it is not surprising that a great many parasites have learned to take advantage of the food-chain system, in truth of the whole food-cycle governing the animal community of which they are members. This means distributing the stages of their life-cycle among two or more hosts, one stage devoted to each. The advantage gained is an enhanced security, a reduction in some measure at least of the extreme chanciness of their existence. In the simpler instances it solves the problem of what happens to the parasite when its host is devoured by a predator, since an essential part of the scheme is that very act of devouring.

To take one of these simpler examples: foxes eat rabbits, and there is a tapeworm infesting both, passing the larval stage in the rabbit and the adult stage in the fox. The cycle is completed when the tapeworm in the fox lays enormous numbers of eggs which pass out with the faeces. These eggs infect the grass eaten by rabbits. The more subtle refinements of this process must not be lost sight of. The larvae and the adult tapeworms do not content themselves merely with entering the bodies of rabbit and fox respectively. The larvae embed themselves in the muscles of the rabbit which the fox can hardly fail to devour, while the adults settle down to a life of ease in the intestine of the fox, from whence the eggs will duly be extruded.

Other examples are distinctly more complicated. A well-known one is that of the liver-fluke, causing a serious disease

among sheep. The secondary host is the water-snail *Limnaea trunculata*, found in damp meadows and riverside pastures. In the course of its long journey from the sheep by way of the snail, and so back into the sheep, the fluke passes through no fewer than seven stages. First comes the egg, passed out onto the grass in the faeces of the sheep. This develops into a ciliated larva, the *miracidium*, which has eye-spots sensitive to light and is capable of moving over the damp grass by means of its cilia. Vast numbers of them die, but the odd one or two come in contact with a snail and bore their way into its tissues. Here they grow quickly and cast their cilia, becoming transformed into a totally different kind of larva, the *sporocyst*. Certain cells within them develop into a third kind of larva, the *redia* with a small mouth and a simple intestine. From the *redia* comes the final larval stage, known as the *cercaria*, a heart-shaped creature about half a millimetre in length and with a wriggling tail. It passes out of the snail once more to the wet world of the grass, encysts itself rapidly, and can survive in this condition for several months depending on the moisture-content of its surroundings. It is then that a sheep may swallow a few of them, when they make their way into the liver, reaching the final stage of the adult fluke. How did the liver-fluke fare, it is reasonable to ask, before man reached the pastoral stage of his development and so provided it with vastly increased numbers of its primary host grazing in damp pastures? Presumably it made use of some wild grazing animal, perhaps the ancestors of our present sheep. Here, as so often, man has provided much more favourable conditions for the pests that afflict him.

Another example of these complex life-cycles is worth giving because it shows more than one point of peculiar interest. This is another fluke, *Distomum macrostomum*, parasitic in the intestine of thrushes. Once more a snail figures as secondary host, *Helix aspersa*, and the food-chain involved is that found in gardens and fields, where thrushes have learned to take snails and crack their shells against stones. Who does not know the calm of a summer garden when the

silence is broken only by the modest impact of snail-shell on stone? Once within the body of the snail the larva of the fluke makes its way to the tentacles, where it produces pigments in bands of red and green. The presence of the larva on the tentacles prevents the snail from withdrawing them, and it is claimed that this makes it all the more conspicuous to the bright eyes of the thrush. So here we have a parasitic fluke that appears to take advantage of a specialized feeding habit of its principal victim, since thrushes do not subsist solely on snails. If the point about the tentacles could be confirmed by experiment, to show that thrushes are in truth more likely to pick out infested snails, it would be clear that the fluke has acquired a means of making its secondary host more noticeable to the primary, truly a wonderful example of adaptation and the use of advertising colours.

These are only two examples of complex parasite cycles. There are others peculiar to their own habitat, making use of the food-cycle pertaining to the habitat. On the sea-shore, for instance, there is yet another fluke, parasitic this time on herring-gulls. Its life-cycle is more complicated than either of those mentioned, for it has two secondary hosts. One is the common periwinkle, the other a small inshore fish called the goby, which herring-gulls are addicted to eating.

One more point must be made, again showing how parasitism links up with ecology. Parasites, apart from pirates and robbers, are necessarily much smaller than their hosts. Many of them are themselves parasitized. Ticks and fleas, for instance, have protozoan parasites of their own. Once more they must be smaller than their hosts. Here then is a food-chain among parasites and hosts, but the pyramid of numbers, instead of being made up of smaller numbers of larger creatures, is here inverted and consists of a larger number of smaller creatures. When the complete food-cycle is worked out showing one or more free-living creatures, together with their parasites and including the parasites on the parasites, some idea of the complexity of these strands of dependence becomes clear.

5

STRANDS OF DEPENDENCE: 2

THE LAW OF MY NEIGHBOUR

Il fauts' entr'aider: c'est la loi de nature.

FRENCH PROVERB

THE preceding chapter was concerned with that form of dependence based on competition. For the most part it was a matter of competition between one kind of animal and another, inter-specific, though this was not so in every instance. One important exception was the territorial system. Owners of territories it is true defend them to some extent against other species, but the greater part of their aggressive display is directed against their own kind, particularly by male against male. The present chapter will be devoted to the other kind of dependence, that based on cooperation. A great deal, perhaps most, of this is carried out between members of the same species, is intra-specific, but again there are notable exceptions My general purpose is to show that cooperative dependence is just as important in nature as competitive, though it has received far less attention. It is only within the last thirty years or so that ways of cooperation, though long known to exist, have been given anything like their due weight in the scheme of things.

To make a somewhat paradoxical statement, if it can be shown that an assemblage of living creatures, in spite of being in keen and often bitter competition, have so organized their way of living as to restrict competition as far as possible, with the result that the resources of their environment are in effect shared, then that way of living deserves to be called cooperative. The food-cycle, even though it means ruthless predation, is a method of portioning out available food. So, even more, is the system of ecological niches, according to

which each species, and each individual within the species, can be reasonably certain of a particular kind of food without having to fight to obtain it. The territory system can be similarly described, resulting as it does at least in some measure of spacing out and avoidance of overcrowding. Where competitive dependence is concerned therefore we find that competition is cut down to a minimum, and this can be achieved only by a truly cooperative general system.

The urge to associate

This is a great deal, but is very far from being all. Cooperation among animals goes much farther, as far in fact as to justify the conclusion that there exists throughout the world of animals an innate and widespread tendency to cooperate, to organize their existence on a basis of mutual aid. This is nothing less than a fundamental ecological principle, and a great weight of evidence can be adduced in support of it. How many kinds of animal are there that live entirely solitary lives, apart from the absolute minimum of coming together demanded by sexual reproduction and the rearing of young? That much cooperation at least is required, and it appeared at a very early date when sex came into the world, among animals low in the scale of development. But for the moment that particular form of cooperation can be set on one side. It is the major predators that appear as sturdy individualists, though not by any means all of them. Raptorial birds live and hunt alone, or at most in pairs. So do some predatory mammals. Among fishes and invertebrates solitude is the rule for camouflaged lurkers waiting in concealment for their prey. For the rest we find a marked tendency towards some sort of flocking, if not all the time then for at least a part of the year. The very existence of those attractive nouns of assembly – a pride of lions, a gaggle of geese, a charm of goldfinches and the rest – is evidence of a sort on its own.

Some kinds of association are highly specialized and intimate, involving animals of widely divergent relationship,

a few, and these perhaps the most interesting of all, extending beyond the boundaries of the animal kingdom to include plants, intimate partnerships between an animal and a plant, or between two plants. Two kinds of partnership of this kind are distinguished, though it is not always easy to maintain the distinction. They are symbiosis and commensalism.

SYMBIOSIS. This is much the more intimate of the two, but the distinction between symbiosis and commensalism is usually drawn, not according to intimacy but according to whether benefit is mutual or one sided. In symbiosis it is mutual. Where two plants are concerned the most notable example is the lichens, whose texture is a close weaving of the threads of a fungus with the green cells of an alga. The fungus, like all fungi, is deficient in chlorophyll but derives carbohydrates from the alga, which does possess chlorophyll and so makes them from carbon-dioxide by photosynthesis. In return for this the fungus provides the alga with water containing nutrient salts. Lichens are of the utmost interest for the animal ecologist because of the part they play as the earliest colonists of a stretch of bare rock, helping to convert it into a habitat for the higher plants, and so for animals. They do much to initiate the progress of a plant sere (see page 152). Then there are the nitrogen-fixing bacteria, referred to in Chapter 2, partners in a symbiotic association with leguminous plants such as peas, beans, and clovers. The bacteria, in nodules on the roots, build up nitrogen compounds from the air and these are used by the plants. As their share of the bargain, the bacteria draw carbohydrates which the plants have manufactured by photosynthesis.

As for symbiotic partnerships between animals and plants, they are to be found in more than one of the provinces into which the animal kingdom is divided. Again the plant concerned is a unicellular alga, and the animals are green for the same reason that plants are green, that they contain these cells provided with cholorophyll. A minute flat-worm known as *Convoluta* appears at low tide over stretches of sand on the

northern coast of Brittany in such profusion as to colour the sand like grass. They rise to the surface in their millions to enlist the cooperation of sunlight in their work of photosynthesis. When the tide begins to turn they submerge, and soon not a trace of verdure is to be seen. Mutual benefits received in this case are of more than one kind. The animal obtains oxygen from the photosynthesis of the plant, and at the same time receives assistance in excretion which gives rise to phosphates. These substances, which are waste products from the animal's point of view, are used by the plant to form protein. Another benefit derived by the plant is a supply of carbon-dioxide, which is a product of the animal's respiration, and to this can be added the protection it enjoys from its close physiological association with the animal.

A very strange feature of this intimate bond is that the arrangement endures only while *Convoluta* is growing. The reason appears to be that during this period it seeks its own food in the form of diatoms and minute animals and at the same time enjoys the benefits derived from its partner. So long as this continues the partnership flourishes, but after a time it takes to devouring its own plant cells and is apparently then incapable of using any other food. The result is that the association is dissolved, whereupon *Convoluta* starves to death. Another remarkable thing about this partnership is that in one respect it is one-sided. The alga is a facultative symbiont, capable that is to say of an independent existence. To *Convoluta*, in contrast, the association of the plant cells is essential.

Another example of this sort of symbiosis, but without its fatal termination, is to be found in one species, or sub-species of hydra, the common fresh-water coelenterate of our ponds and ditches. These creatures are green and mutual benefits derived are the same as with *Convoluta*. There are yet more among some of the corals of tropical seas, and among sponges of temperate waters. A very strange example of symbiosis is found among many of the termites, which subsist on a diet of wood. This seems to us an unsatisfying

food, and so it is even to the termites, which are incapable of digesting it without the cooperation of flagellate protozoa living what appears to be a parasitic existence in their digestive tracts. The protozoa render the wood available both to themselves and to the termites, who if deprived of their assistance, as can be done by applying heat, die within twenty days.

But symbiotic relationships need not be confined to animals and plants, nor need they be as intimate as in these examples. If they are understood as partnerships in which mutual benefit is conferred, many other examples could be given, though it is not always easy to be sure that mutualism exists. There is for instance a beautiful and delicate sponge of Far Eastern waters, *Euplectella aspergillum*, more commonly known as Venus's Flower Basket, that harbours a small crustacean, *Spongicola venusta*. The method of feeding adopted by sponges is to draw water within their tissues by means of the currents they set up. With the water come minute organisms on which they feed. So in this instance it can be supposed that the crustacean finds easy subsistence on these trapped creatures, while the sponge benefits from the scavenging activities of *Spongicola*. What conclusions can be arrived at with regard to a small fish found frequently sheltering under that highly specialized jelly-fish *Physalia*, the Portuguese Man-of-War, with its extremely formidable stings? The fish, apparently immune from the stings, gains shelter: it is less easy to see how *Physalia* benefits, unless the fish acts as a decoy to other fish.

A not uncommon association between animals is when one lives and grows upon another, and the smaller partner is then known as an epizoite, just as a plant growing upon another plant is called an epiphyte. This may lead to parasitism, but an epizoite lives on its own resources and not at the expense of its host. It is a common form of association in the sea and in fresh water, and some instances may well be symbiotic. In the Indian Ocean there lives a small rock perch, *Minous inermis*, which never seems to be free from a heavy infestation of hydroids. It looks as though the hydroids help to conceal

the perch and in so doing achieve a mobility denied to most of their kind. A delightful and very remarkable refinement of the symbiotic way of life has been perfected by a crab of the genus *Melia*, again from the Indian Ocean. This apparently sagacious creature has taken to plucking certain small sea anemones from the sand and swimming about with one of them clasped in each of its pincers. When the anemones catch food, after the manner of their kind, from the surrounding water, *Melia* extends one of its first pair of walking legs and removes what it considers to be its share. If this is indeed an instance of symbiosis, we may suppose that with the anemones the advantage is that gained by transport.

Passing to dry land, we find a number of associations among larger animals in which benefit appears to be mutual. Most of us have seen starlings perched on the backs of cattle and sheep. If, as seems highly probable, their purpose is to remove keds and lice, then this is a simple symbiotic relationship, the starlings gaining food and in doing so helping to relieve the sheep of the parasites that afflict them. There is no doubt about similar services rendered by the ox-pecker birds of the African savanna to the large grazing animals on whose backs they spend most of their time, running about all over them like mice, subsisting it seems entirely on ticks, biting flies and lice It is said that they depend also for their nesting material on the coarse hair of their hosts, who clearly welcome their attentions, though it appears that there are occasions when the birds peck at wounds in the buffaloes' hide, and in so doing become parasites rather than symbionts.

An interesting instance of association between animals of yet more widely divergent relationship occurs where birds and formidably armed insects nest close together. There is for instance the boldly coloured yellow-backed oriole which has formed the habit of building its nest almost touching the large nests of wasps. The wasps, it can be supposed, serve efficiently to keep off egg-thieves, while it has been suggested that the presence of the brightly coloured birds act as a warning to intruders of the stings of the wasps.

All these, though to the highest degree strange and interesting, are no more than isolated examples of mutually beneficial association. If the device has proved to be a success we would expect to find one or more particular pattern of partnership illustrated by a considerable number of examples. In this expectation we are not disappointed, for there has come to light in recent years an instance of this very thing. The simplest term for it is 'cleaning symbiosis', and it can be thought of as closely parallel with the partnership between ox-pecker birds and hoofed mammals just referrred to, in which one partner gets its living by removing parasites from the other. This form of symbiosis is comparatively rare on land, but in the sea, more especially in tropical seas, it is now known to be common and widespread, to be regarded not merely as a bright idea perfected by a few, but as one of the primary relationships governing life in the sea. No fewer than twenty-six species of fish are known to devote most, though not all of their time, to the systematic cleaning of other fish which welcome and eagerly seek out their services. Six species of shrimp do the same and at least one crab. To mention only one example, there is the golden-brown wrasse (*Oxyjulis californica*) of southern Californian waters, popularly known as the *señorita*, which clears both of parasites and of dead tissue waiting throngs of the opal eye (*Girella nigricans*) as well as those of three other species.

This, as I have said, is a new discovery and there is no doubt that many more examples will come to light. For all its newness it has already yielded basic and far-reaching principles. Cleaning fish, for instance, of otherwise unrelated groups have evolved convergently, so as to acquire pointed snouts and teeth resembling tweezers. All are brightly coloured and boldly patterned, conspicuous against their background. To enhance the effect, some of them indulge in characteristic intention-movements, attitudes, and gyrations deserving to be called advertising displays. The services of cleaners are so highly valued that predatory fish leave them alone, and in consequence there have arisen non-cleaning impostors who have found it worth while to imitate them and so share the

security they enjoy. Finally it seems that particular localities are set apart as 'cleaning-stations', resorted to from considerable distances by various kinds of fish in need of cleaning. This must mean that cleaning symbiosis plays a part of some note in determining the distribution of tropical fishes.

COMMENSALISM. The word means feeding together, and it is commonly stated that one of the partners benefits and not the other. The following examples illustrate this point, if on occasions rather doubtfully, while some multiple associations combine examples of symbiosis, commensalism and parasitism. As such they may be inconvenient for the systematist, but are of particular interest for the fact that they show this combination.

Consider for instance the well-known case of the hermit-crab which has soft and very vulnerable hinder parts. These it protects by inhabiting a cast-off whelk-shell. Frequently the shell, thus serving a secondary phase of usefulness, is found to be densely encrusted with polyps of the hydroid *Hydractina*. This could be construed as symbiosis, since the hydroids gain transport, perhaps protection and an enhanced food-supply, while the crab is camouflaged by the growth on its shell. The same could be said of a sea-anemone, *Adamsia*, often found on a hermit-crab's shell (Plate 2a) known to bend over when the crab has conveyed it to a particularly rich feeding-ground and sweep the floor with its tentacles. The crab, on its side, gains protection, or so it is reasonable to suppose, through the stinging tentacles of the anemone. Another associate of hermit-crabs is a bristle-worm of the genus *Nereis* which emerges to share in the crab's food. This looks like commensalism in which one partner enjoys all the privileges, but it is possible that the worm is something of a scavenger in the recesses of the shell, in which case the association is symbiotic.

As another instance of the difficulty of making the convenient and rigid distinctions beloved of the human mind, the very remarkable life-history of the large blue butterfly, *Maculinea arion*, can be cited. This is one of the most astonishing of all

animal associations, among other reasons because the larva of the butterfly is free-living for part of its existence, commensal and in a distinct sense parasitic for the rest. The large blue lays its eggs on wild thyme in a downland habitat, and the larva feeds on the thyme, living on its own up to the time of its third moult. After that a change comes over it. It begins to wander about as though looking for something. So it is. It is looking for an ant, having reached a crisis in its life of such urgency that if it fails to find an ant it will perish. At the same time it now possesses an inducement for an ant to play its part in the strange sequence of events that follow, for it has by this time developed a honey-gland secreting a sweet fluid of the sort for which ants have a passion. Ants are by no means uncommon on the chalk downs, and the likelihood of the encounter taking place is considerable, especially as there is evidence for supposing that the butterfly usually lays her eggs at no great distance from an ant's nest.

As soon as the meeting takes place, the ant is sure to take a lively interest in the caterpillar, and the interest is welcomed. The caterpillar makes this clear at first by allowing itself to be milked, later by hunching itself up into a curious attitude, as though asking to be picked up. The ant responds as it was meant to, and presently carries the caterpillar off to its nest. It is in the darkness of this alien nest that the rest of the metamorphosis is worked out. Up to the time of its winter hibernation and afterwards, until it pupates, the larva feeds solely on the grubs of its hosts, the ants, who display not the least resentment, apparently considering themselves amply paid by the sweet liquid of the honey-gland. This comes very close to symbiosis, though the caterpillar seems to have the best of the bargain. In the following summer this strange messmate, having emerged from the pupa, emerges also from the ant's nest to the open air, where its wings expand and it becomes a free-living butterfly.

Remaining among the ants we come upon another association of this commensal sort, and one that involves something much more than mere commensalism. The larva of the large

blue butterfly is only one of the creatures that secretes a sweet fluid irresistible to ants. Notable among these are the aphids or greenfly, and it has been known for many years that these have come to mean so much to certain ants, among them the small black or garden ant very common in this country, that they have become pastoralists, solicitously tending herds of aphids that are regularly milked and put out to pasture, like so many cows, on suitable plants not far from the nest. Some kinds of aphids are kept in special compartments of the nest underground, where they subsist on the sap drawn from the roots of grasses. Some writers have made out that the benefit derived by aphids from this protection has saved them from extermination. Some degree of protection is not to be denied, and aphids are defenceless and extremely sluggish creatures, preyed upon to a devastating extent, but we are probably on surer ground if we attribute their survival to their prodigious powers of reproduction.

Many other creatures besides aphids are to be found in the nests of ants, particularly in those of the wood-ant that builds up those familiar mounds of pine-needles in coniferous woods. Some of these are tolerated and indeed welcome guests, valued once more for the fluids they secrete. Others are scavengers feeding on refuse. A third category cannot be called guests and are parasites, devouring the larvae and pupae of the ants which make vain attempts to eject them. But the marauders defend themselves by shooting out fluids not sweet but offensive. There are upwards of 300 of these myrmecophilies in Britain alone, most of them beetles of various kinds, though the larvae of some of the hover-flies are included as well.

There are examples of commensalism among vertebrates. A remarkable one is that of a certain South American parakeet, which builds its nest and raises its brood in the carton-nests of a species of termite and will do so in no other situation. When the birds arrive and begin to hollow out the termitary, the termites rush out to repair the damage, but quite soon change their tactics and decide to leave the birds alone. It would be wholly within their power to attack the nestlings subsequently,

but this temptation too is overcome. In this instance it is clear enough what the parakeets stand to gain, since egg-thieves are likely to respect termites. What the termites gain, if anything at all, it is impossible to say.

Again among vertebrates, is the well-known association between blue sharks and pilot-fish. Some of the stories concerning them are no doubt legendary, but the association exists. A more intimate one is that between sharks and remoras, which are equipped with suckers for their very firm attachment to their hosts. This suggests parasitism, but there seems to be no evidence that the remora derives nourishment directly from the shark. We may suppose that it gains transport and perhaps scraps from time to time from the host's table. The shark on the other hand seems to gain nothing.

WIDER CONSIDERATIONS OF THE URGE TO ASSOCIATE. Examples of symbiosis and commensalism, so far as they are distinguishable, are of the greatest interest, and no more than a few examples have been cited. But for all their interest and strangeness they are isolated, specialized, and concerned with partnership between differing species of animal. Cleaning symbiosis is much more than this. Nevertheless if reliance were to be placed upon that, as well as upon the isolated examples of symbiosis and commensalism, as evidence for the assertion that the tendency to associate for cooperative living is a fundamental ecological principle, no very convincing case could be made out. It is to other and far commoner examples that I must now turn, those for the most part between animals of the same species; for though the lying down together of the leopard with the kid may be the symbol for cooperation in an idealized world, in the words of the prophet Isaiah, in the world of nature we shall be more likely to find it in the lying down of leopard with leopard and of kid with kid.

We should, I suppose, begin not with complete animals, but with the millions of cells of which every individual animal is composed. The cells crowd together cooperatively to form tissues of muscle and fibre, while tissues associate similarly to

build up organs, and organs in their turn to build a living body. But perhaps it is more relevant to the subject to consider first the isolated cell that, even in its isolation, is an animal on its own. I mean of course the one-celled animals, the protozoa. Scarcely any of them can be said to lead a solitary existence, and their association is of two distinct kinds: in the first place a crowding together of millions into a swarming aggregation, in the second the actual contact of a number of cells or individuals to form a composite organism, not yet a many-celled creature but an organism of the kind usually known as colonial.

An example of the first is *Paramoecium*, the slipper animalcule visible in a drop of water under the microscope. These swim by means of their rippling cilia, each one on its own but in company with scores of its fellows, and on occasions meeting one of them in a conjugation, which is among the earliest intimations of sex, and appears to be necessary for the renewed vigour of the stock. A more striking example is the minute green creature, *Euglena*, one of those borderline, plant-animal organisms, that assemble in milling swarms in such astronomical numbers as to colour with vivid green the contents of a water-butt or even of a pond. Some protozoa are fixed, with a bell-shaped body at the end of a long stalk. But the stalks have a common attachment (Plate 2b). *Vorticella* for instance bunches in what looks like a tangled knot, each bell on its own, waving its aureole of cilia independently, but clearly indicating the bond uniting it with all the others by the way each, in concert with the rest, twitches back in sudden withdrawal, spiralling its stalk corkscrew-fashion, when the composure of the colony has been disturbed. Such forms are intermediate between the free-swimming protozoa and closely united, colonial organisms such as *Volvox*. This must be reckoned as a plant in the form of a hollow sphere made up of hundreds of green cells, all united into a network so as to resemble an emerald of a hundred facets.

Aggregations again of two kinds are found frequently rather higher in the scale, among the coelenterates which are true many-celled animals. There are the sea-anemones, encrusta-

tions of hydroids like pygmy forests covering the surface of rocks, companies of medusae or jelly-fish, branched bosses and knobs of coral. In the same division of the animal kingdom we find colonial forms of a much more complex kind in which the various members of the colony are not single cells, but are distinguishable according to the function they perform for the organism as a whole. Of these the most notable examples are those extremely delicate creatures the siphonophores, found floating on the surface of the sea, each one consisting of integrated polyps, or as they are sometimes rather pleasantly called, persons: feeding persons, protecting persons, armed with stinging cells, reproductive persons giving rise to buds of medusae which detach themselves, as well as persons whose precise function in the colony remains something of a mystery.

The ctenophores or comb-jellies, which are not coelenterates but are grouped into a phylum of their own, are often found in immense swarms. Many of the marine worms tend to group into aggregations, some of free individuals like the beautiful peacock worm (*Sabella pavonia*) growing in thickets, each in its tube and protruding its circular halo of tentacles; or on the other hand massed into hard bosses, like the reef-building worm (*Sabellaria alveolata*). The echinoderms, that phylum to which star-fishes and sea-urchins belong, are much given to gregarious living, brittle-stars on the sea-floor, and in particular the delicate crinoids, feather-stars, or sea-lilies, crowded like flowers in some herbaceous border.

Among marine molluscs aggregation becomes almost a rule, at least among the commoner forms. Lift up the wet fronds of fucoid seaweeds at low tide and you will find flat periwinkles in threes and fours to every frond, brown, yellow, and banded. Dog-whelks and top-shells prefer one another's company. So do the rough periwinkles, and that smaller member of the same genus, both found at and often above the limit of high spring tides. All seaside holidaymakers know the common limpet, closely crowded over the rocks, inert and immovable when the tide is out, browsing over contiguous territories when the sea covers them. There are close-packed beds of oysters,

and aggregations of mussels so dense as to cover one another. Among crustaceans the larger ones are apt to be solitary, but minute copepods, in uncountable millions, contribute notably to the plankton both in salt water and fresh, while everyone knows the throngs of that strange sessile crustacean the acorn barnacle (Plate 10a and b).

Passing to dry land we find a similar social appetite well developed and widespread among insects – swarms of midges on summer evenings, companies of mayflies along river-banks newly liberated from the aquatic larval stage and wavering like snowflakes in a flurry of wind. Among insects, as well as other animals, we find one of three special reasons for the urge to flock: for breeding, as with midges and mayflies; for passing the winter months in hibernation, as with those companies of ladybird beetles so often found under leaves; for migration, as with locusts and many kinds of butterfly. Association for breeding purposes is extremely common among fishes, among frogs and toads. Some fishes, notably the herring, seem to crowd together in shoals for the whole of their lives. At times the purpose is spawning, at others feeding on correspondingly dense aggregations of plankton. Feeding in fact deserves to be reckoned as a fourth reason for flocking.

Most birds prefer relative solitude during the breeding season, marking out territories, as described in the last chapter; but these, or many of them, tend to flock during the rest of the year, frequently in company with other species, quartering the woods in a search for food. Birds do not hibernate, but among them we find the flocking tendency used for every other purpose – breeding flocks, as with rooks, herons, gannets and many others; migrating flocks, probably with every kind of bird that migrates at all extensively (Plate 3a); feeding flocks, as with tits in the winter, with starlings in a field and most kinds of wader, following the ebbing tide, probing in the sand as they go; and yet another reason, roosting, as with starlings, on occasions in such numbers as to resemble clouds of billowing smoke.

I began by giving three reasons for the flocking urge: repro-

duction, hibernation and migration. I then added a fourth, feeding, and subsequently a fifth, roosting. I now succumb to the temptation to add a sixth not unknown, that which to all appearances is nothing but sheer enjoyment or play. The specific playmates I am thinking of are lapwings that I watched for upwards of an hour one September afternoon. The scene was a reservoir surrounded by fields of arable and pasture, and the lapwings varied in number from thirty or so up to well over a hundred, for it seemed that neighbouring flocks, seeing the fun that was going on, decided to join in. It was mainly over the water that they were disporting themselves, and their play took the form of sweeping low over the surface, to within a few feet. What a gay fluttering of pied wings it was, as they swooped, tumbled, and twisted, often making steep, banking turns. Occasionally one bird would shoot fifty feet and more vertically upwards, then come twisting down. For most of the time they were strangely silent and at no time did I hear the familiar, plaintive pee-wee, or at most a soft piping no more than faintly reminiscent. Once or twice so exuberant did they become that a passing black-headed gull, or a jackdaw, was playfully mobbed and chivvied from the scene. Once a pair of great crested grebes, placidly swimming, was treated in the same way, but this time without result.

Mammals must not be omitted, though many of the examples of the social appetite among them are almost too well known to be worth mentioning – the great herds of antelopes and zebras of African savannas; of bison that similarly roamed the American prairies until advancing civilization wiped them out, save for the present pitiful remnants; of caribou that still migrate in hordes over the Canadian tundra, soon no doubt to go the way of the bison. Bats of most kinds both roost during the day and hibernate during the winter in large gatherings. As for the other small mammals we have only to think of rabbits before myxomatosis, lemmings, shrews, field-mice, most of them at times reaching plague dimensions from our point of view.

The point need not be laboured, if I have not already done

so. More important is to inquire closely into the object of this social appetite. That there exists some object other than the direct ones of reproducing, migrating, feeding, and the rest must surely be granted. There can hardly fail to be biological advantages in so widespread and noticeable a tendency, and those advantages can be expressed generally and singly as something that enhances the welfare, helps to ensure the survival, not of individuals so much as of species, or perhaps more accurately of the aggregations so brought together.

SURVIVAL VALUE OF THE URGE TO ASSOCIATE. Where feeding is concerned the object seems obvious enough, but we can go below the obvious in pointing out that insects, for instance, dislodged from the grass by a flock of feeding birds, might well be disturbed in greater numbers from the point of view of each bird than if it were feeding on its own. The same would apply to the winter flocks of tits and finches in a wood. Starlings have perfected an admirable method of communal feeding. The flock, probing among the tussocks of a field, acts as a flock, maintaining a constant direction of movement, and so that there shall be fair shares for all, the advancing front is continuously augmented by birds from the rear flying over the backs of their companions. In this way every bird has its share of unexplored ground. Collective security against predators certainly plays a part. Instances are well known of flocks of feeding or of breeding birds ready to take alarm from sentinels, who utter a specific and established danger-signal. A rather special instance of massing for collective defence has been suggested, almost certainly on good grounds, in the close-packed flickering swarms of the minute crustaceans, *Daphnia*, in almost any pond. These might well produce a bewildering effect on a predatory stickleback confronted thus with an embarrassment of riches. A few stragglers on the outskirts may be snapped up, while the main body enjoys an immunity that would be denied them if they were widely dispersed. The same purpose might govern hordes of migrating butterflies, or even of some birds.

There may be an element of defence in the communal roosting of starlings, though it seems unlikely, and it could hardly apply to bats who appear to be free from predation. As for hibernating ladybirds, snails, or once more bats, it is difficult to think of any underlying significance, even that of added warmth, since the first two are cold-blooded at all times, while the warm-blooded bats become cold-blooded when they hibernate. As for play, it is well known among many young mammals, foxes, and badgers for instance, and its biological purpose, as with our own species, is a limbering up of muscles and a preparation for the battle of life. Among adult animals it is less common although otters, as well as other, larger animals, have been recorded as having the greatest fun on a mud-slide on the banks of a river. These tobogganing parties are made up of both young and old, and it is difficult to see what object there can be apart from amusement.

That leaves gatherings for breeding purposes (Plate 3b), in some ways perhaps the most important of all. This is so widespread a custom, so successful and regularly maintained by natural selection, that we are surely justified in concluding that considerable advantages accrue from it. Common defence once more, on the principle of there being safety in numbers, may come into play, but this is not altogether convincing, since gregarious nesters, such as rooks, gannets, and herons, are not victimized by predators to any marked extent, unless indeed for that very reason. But after all the over-riding purpose of these gatherings is reproduction, so it seems logical to suggest that it is there that we shall find the answer.

This leads at once to one simple explanation. Breeding associations of all kinds result in a meeting of the sexes, in such a way as to increase the probability of each male coming in sexual contact with a female. In that way there will be fewer unmated individuals in any local population of the species. With fishes and amphibians, with a few exceptions, fertilization is external, the females depositing eggs, which the males subsequently fertilize. Where communal marriage rites are concerned this sequence of events is more likely to occur with regard to

every individual in the gathering. Where fertilization is internal, involving some sort of mounting of the female by the male, the gregarious system has added importance.

The same principle will operate both in the sea and on land. It will operate even among those sedentary creatures that shed their gametes – eggs and sperms – into the water, depending on the relatively remote chance of their meeting. Eggs are generally inert, sperms endowed with the power to move. The sperm has to seek out the egg. But an unfertilized egg has a very short life, and the active range of a sperm is probably no more than a few feet. Hence the likelihood of the two coming in contact is enormously enhanced if the adults that extruded them live in close association with one another.

But is there more than this? Can it be said that efficiency of reproduction is increased by close association of breeding pairs? In one or two rather specialized instances there is little doubt that it can. There are some birds, ruffs* and blackcock for instance, that stage gatherings of both sexes at the start of the breeding season, in which courtship displays of the cocks before the hens figure very prominently. There seems to be little doubt that sexual selection in the Darwinian sense takes place at such gatherings, the hens showing preference for the more extravagantly displaying cocks. Apart from this, it is possible that each nuptially adorned and posturing cock contributes to a sexual stimulus affecting all the rest.

The Scottish biologist and writer Dr Fraser Darling is prepared to go farther than this, though it must be added that his conclusions have been questioned by others. He is convinced that the massed presence of many animals, notably black-headed gulls and fulmars, produces a common stimulus to breeding activity which increases with the size of the colony, that large colonies begin laying eggs earlier in the season, and that the egg-laying period is shorter in a large than in a small colony. In the life of a gull the most critical period is that from the hatching of the egg up to the end of the fledgeling stage. At this time chances of survival are at their lowest, not only from

outside predators, but from other members of the breeding colony as well, since wandering chicks are liable to be attacked often with fatal results. It appears that a relatively short fledeging period corresponds to a relatively short egg-laying period, that in consequence a greater number of fledeglings are likely to survive in a large colony than in a small one. A further conclusion is that there is a limit to the size of a colony below which breeding will not take place at all.

This theory of social stimulation in breeding colonies has received some confirmation. If it could be applied to all animals that breed gregariously, its importance becomes obvious. Certainly it is a theory one would like to believe in, though that of course is a thoroughly unscientific attitude. Every theory must be subjected to an exacting series of tests before it can be accepted. In science faith counts, or should count, for nothing. Scepticism is what matters, at least until a theory is generally accepted. Even then a modicum of scepticism is all to the good.

COOPFRATION AMONG ANIMALS. The statements just made about scepticism and the importance of testing a theory, applicable everywhere, are particularly applicable to what follows. The truth is that this basic idea of cooperation has been closely bound up with one man, the late American biologist W. C. Allee, and the pages that follow owe everything to his book *Co-operation Among Animals*. I am not suggesting that Allee was given to theorizing without checking his theories by means of controlled experiments. On the contrary his findings were confirmed repeatedly by laboratory experiments, as set out in his book. What I mean is that these far-reaching, not to say revolutionary, findings have not yet received general acceptance. The century-old conception of the savagery of nature, of a relentless struggle for existence, in which only the fit survive, is still firmly implanted. Any theory which, though far from denying its existence, insists that we have made too much of the struggle for existence, and invites us to give equal prominence to a conception based on cooperation, is bound to be rejected

by many. Let me repeat that the idea of cooperation does not rule out the idea of a struggle for existence. In effect it gives the struggle a wider validity, insisting that bitter inter-specific competition is by no means the sole governing principle, that the life of animals is guided and governed by competition on the one hand and cooperation on the other. Natural selection operates with regard to both. The ceaseless warfare between predator and prey gives advantage to the efficiently armed, the efficiently protected, and the efficiently elusive individual, and so to the species: the principle of cooperation, on the other hand, gives advantage to the efficiently integrated social group or aggregation of many individuals of the same species, whether that aggregation is loosely bound together like a population of *Euglena* in a pond or a breeding colony of gannets; or whether it is a highly organized social unit like a nest of wood-ants or a hive of honey-bees. Competition and cooperation are complements of one another, go hand in hand. If this book of mine has a theme above others that is it, together with the fundamental unity of nature, the indissoluble alliance between plants and animals, soil and climate, earth and air.

The idea after all is not altogether new and I have referred to it already. In the chapter on competition, when dealing with the subject of density, I pointed out that, while ecologists have long recognized that overcrowding is bound in time to lead to disaster, almost equal hazards are attendant upon too small a number, that there is such a thing as undercrowding. The thought is inherent also in Fraser Darling's notion of benefits conferred by the mere fact of association as in a breeding colony of birds. What Allee has done is to lay added stress upon, and to extend much more widely, this conception of undercrowding. What emerges is the importance of an intermediate state of affairs, an optimum density.

Beginning with the notion that there is prosperity in numbers, Allee demonstrated that ten goldfish swimming in a dilution of colloidal silver, a substance poisonous to fish, survived over twice as long as one goldfish swimming by itself in a dilution of the same proportion. The explanation arrived at was that the fish

gave off a protective secretion; that, though this secretion was in neither case sufficient to immunize them from the poison, ill effects could be postponed for more than twice as long when ten fish could share in the secretion given off by all, as when there was only one to benefit from its own unassisted efforts.

Similar results were obtained with flatworms exposed to a physical hazard, in this case ultra-violet radiation. This caused the worms to disintegrate, but more quickly if isolated than if grouped. Yet another series, again with flatworms, showed that they live longer if placed in water that has been conditioned, in a sense contaminated, by the previous presence of dead worms of the same species, than in water not so conditioned. Similar results are obtained when a quality they require is absent as when some other quality, inimical to their welfare, is artificially introduced. In the last experiment the thing that was absent was an element normally present in their environment, and it is now known that this element is calcium. Dead and disintegrating flatworms, it seems, as well as living ones though more slowly, give off calcium into the surrounding water.

On another occasion the eggs of a common sea-urchin were used. When one of these eggs has united with a sperm it divides into two after fifty minutes. This is known as the first cleavage and is the initial step in the development of an adult sea-urchin. About half an hour later there is a second cleavage, to be followed by others in relatively quick succession. After twenty-four hours of this process, complicated by other processes, a complete larva appears. The experiment showed that the period from fertilization to first cleavage, and after that to the second and third, was appreciably shorter when eggs were present in a relatively crowded state than if few were used. Even more revealing was an experiment with the ciliated protozoan *Oxytricha*, which showed that reproduction, which is asexual as in most protozoans, reached a certain level when a limited number was used, but that this level was lower when a smaller number took part, and was again

lower with a number larger than either of these. In other words the significance of an intermediate or optimum density was clearly demonstrated.

Experiments in the growth-rate of higher animals showed similar results with regard to optimal density. White mice, for instance, were found to grow at a higher rate when in comparatively small than in larger groups. But the lowest rate of growth was obtained with a solitary mouse. That this was not brought about by individual differences in growth-rate from one mouse to another was proved by repeating the experiment with the groups sorted differently. An experiment with flour-beetles of the genus *Trilobium* was of special interest because it was carried out with the beetles in their normal environment, namely flour, and was linked up with one of their normal habits. It was found in the first place that these beetles reproduce more rapidly if a number of pairs are kept together than if one pair is isolated. But two opposing tendencies were at work. One was the rate of egg-laying, together with the laying of a higher percentage of fertile eggs, both of these being increased by repeated mating. The other was the tendency of these creatures to devour one another's eggs, this of course also increasing with the number of beetles present. The interesting point was that the working out of these two opposing tendencies gave rise to an optimum density in which more young were produced than in less or in greater densities.

Allee goes on to discuss the behaviour of animals when loosely associated, or when bound together in some more or less organized social unit. He describes a number of experiments showing that such behaviour is in the first place brought about, in the second stimulated, by their social appetite or tendency to flock. This tendency may or may not have survival value for the species concerned, and is demonstrated in such things as the feeding capacity of fish, the rate at which ants work, the speed with which cockroaches learn to find their way through a simple maze, the extent to which fish are capable of imitating one another. Results obtained were not wholly

consistent; but the cautious general conclusion was that in such vital processes as breeding behaviour, feeding, working, and learning, the presence of companions frequently has a stimulating effect, though in some instances the tendency was in the opposite direction.

This leads to the important problems of the nature of organized units among animals, of what it is that distinguishes social from non-social behaviour, and finally of the evolution of the highly organized colonies such as those of the termites and insects of the bee order. Investigations led him to conclude that an innate social appetite, or as he frequently calls it proto-cooperation, runs right through the animal kingdom, showing itself first among the protozoa. This social appetite brings with it certain advantages, has survival value, and accordingly tends to be preserved by natural selection. In many of the higher animals we find the beginnings of organization showing itself in the formation of graded hierarchies. For instance it is well known that in a flock of hens the individual birds are distinguishable by a peck-order. The dominant bird pecks all the others with impunity. The next has the right to peck all except the dominant bird, and so on down to the lowest which enjoys no pecking privileges at all and is pecked by the whole flock. Qualities making for these distinctions, as we would expect, are maturity, strength and health. Among gregarious mammals dominance arises in a different way. A herd of red deer is a matriarchal society, leadership resting with an old and experienced hind, and a sort of nucleus of the herd is made up of hinds and their young, with the stags attaching themselves loosely during the rutting season. Among monkeys and baboons the leader is more likely to be a male who, while tolerating the presence of one or two other males, drives the rest away.

WHAT MAKES SOCIAL BEHAVIOUR? Considering these and other examples of organization it is natural to ask what it is that constitutes social behaviour. Some would say the distinguishing feature is some form of division of labour, others that it is

nothing more than a broadening of family life. But perhaps the simplest as well as the soundest view is that when animals behave differently in association than they do when isolated from their kind, then their life is to that extent social. But whichever view we take we come once more, as always, on that principle of gradualness of transition emphasized in the first chapter of this book. We find no well-defined dividing line between social and non-social. The one state of affairs, from species to species, merges by a series of gradations into the other. Division of labour, for instance, is of the utmost importance in the most highly organized social units to be found among animals, the city-states of termites, ants, and bees. So deep does it go that it corresponds with marked structural differences between the citizens, producing the caste-system of, for instance, queen-ants, worker-ants, soldier-ants. But division of labour is found among some of the damsel-flies, the male grasping and sustaining the female as she lays her eggs in the water. Are we therefore to reckon damsel-flies among the social insects? Only to the extent that egg-laying is usually carried out by several pairs at the same time.

As for the evolution of the sexual aspect of animal societies it has been shown that one important phase of development has a direct relationship with crowding. The Cladocerans, a large group of aquatic crustaceans, of which *Daphnia* is a member, habitually lay eggs that need no fertilization, but develop directly into females. These females lay eggs that give rise to others of the same sex. But on occasions both males and females appear, and the eggs resulting from their union have survival value because they are hardier, more resistant to adverse conditions such as frost or the drying up of ponds. The most effective way of bringing about the emergence of both sexes is to crowd females more closely together. It is worth pointing out that in nature the onset of adverse conditions would inevitably cause some degree of bunching.

THE SOCIAL INSECTS. Another connexion between social

life and sex is this: when, of the two sexes, one can be shown to be more socially inclined than the other, it is the female of which this is true. The societies formed by bees, ants, and wasps are matriarchal societies, the affairs of the state being carried on by the females, whether egg-laying queens or sterile workers. Males are tolerated only because of their ability to fertilize females. When that job is done they die or are ruthlessly killed off. Among termites on the other hand the two sexes are on a par as regards social proclivities. There are queen-termites and king-termites, while the workers are either sterile females or sterile males. Are termites for that reason more fully organized, higher in the scale of social evolution than ants, bees and wasps? They might be considered so, and yet structurally they are more primitive insects than the Hymenoptera. Termites could be called socially-minded cockroaches.

While on the subject of termites, and considering the whole problem of the evolution of the social way of life, another important point can be made. For most of them social existence is much more than an advantage: it is an absolute necessity. When dealing with symbiosis I referred to the intestinal protozoa without which they are incapable of digesting their food. But each time a termite moults it loses its protozoa, and consequently is faced with starvation unless it can re-infect itself with these essential guests. This it does by devouring the excreta of its fellows. It seems reasonable therefore to regard this obligatory symbiotic alliance as an important factor in the evolution of social organization among termites. The two factors, an innate tendency towards some sort of loosely integrated communal existence, and the harbouring of symbiotic protozoa, could both have been present among the ancestral termites, and in their further development the two could have evolved concurrently, each stimulating the other, each necessary to the other's existence. Just how the caste-system came into being is a separate and much more difficult problem.

Assuming that there is something to be said for this theory of the evolution of termite societies, it is natural to inquire

into its possible application to those of other insects. Is there any parallel in the form of a special inducement towards living together, where ants (Plate 4a), bees, and wasps are concerned? Among ants there is an inducement and it is found in their system of mutual feeding. Worker ants are busily employed, among other activities, in feeding the larvae. This they do by regurgitating whatever they have been able to find on their foraging expeditions. They do not go unrewarded, for the larvae exude a sort of sugary saliva exceedingly palatable to the workers, who eagerly lap it up. This mutual feeding, or trophallaxis, is widely practised, and becomes the outward indication of the bond that unites them. But their feeding habits are communal in another way, for it is the business of the workers to supply the colony as a whole, not the queens and the larvae only but each other as well. Ants are forever licking one another for the sake of this communal food stored in their crops, which are compartments of the alimentary system capable of wide distension, and termed, very aptly, social stomachs. There can be little doubt that both these forms of mutual feeding play a very important part in the economy of ants. Could they have played a part in the evolution of their economy as well? The answer might be that it is the result and not the cause of their intricately organized societies. In its present highly developed form no doubt this is true, but that need not mean that some rudimentary form of it was not present at an early stage and helped to bind ants into societies. Having ventured upon that statement, it is a little disconcerting to be compelled to admit that trophallaxis does not appear to be known among bees.

This flocking urge, this social appetite, which Allee raises to the status of an ecological principle of the first importance, can hardly be ignored. I have pointed out that it can have a variety of purposes, both superficial and underlying, and that in many instances we can trace distinct survival values. His experiments confirming its existence are remarkable, but they have one serious handicap. They are experiments conducted in the inevitably artificial surroundings of the laboratory, where it is

impossible to reproduce natural environments. That Allee was well aware of this deficiency is clear from a section of his book devoted to instances drawn from animals in their natural habitat that he had been able to find. But they do not amount to very much, and what is urgently needed is a series of experiments carried out in the open air, in forests and grasslands, in salt water and fresh. Only there can the subject be fully explored. The trouble is that the difficulties of carrying out such experiments, of isolating the members of any one species, of transferring those rigidly controlled conditions essential to such an investigation from the laboratory to the field, are so great as probably to be insuperable.

6

SOME ANIMAL COMMUNITIES

What's good for the bee is good for the hive.

ENGLISH PROVERB

TWO chapters have now been devoted to the various ties binding animals to one another, ties on the one hand competitive and on the other cooperative. Logically the next step is to gather these together, to make some attempt at describing their interaction so far as it can be seen at work among animal communities of various kinds. I must make it clear that this is a very tall order indeed, that the expression 'making some attempt' is no empty one, and that the attempts made in the following pages will fall very short indeed from being complete. The reason for this is no secret. The web of life is so complex that it is doubtful if any ecologist has yet succeeded in working out the complete food-cycle corresponding to a habitat more extensive than a few square yards of heathland, the shallows of a pond, or a rock-pool abandoned by the tide.

No single worker could hope to describe the intricacies of the complete web over a wide area, giving due attention to food-chains, niches, parasite-associations, territories, oscillations between predators and prey, sub-social aggregations of one species, the links binding one such aggregation with others and all the rest. A team of workers would be needed, continuing their investigations over a period of years, assisted by another team of expert identifiers for all the lower and smaller forms of life concerned. The work would be slow, laborious, and costly; the first stage no more than the amassing of an immense amount of data, to be followed by a second taken up with correlation point by point and each point with the whole. Ecology is still a new science, and it is only within the last twenty to thirty years that its complexity has been realized. Some aspects are of great economic importance, for instance the food-cycle in the sea,

bound up as it is with the fishing industry. It is not surprising therefore that long-term investigations have been subsidized by government departments and conducted, not in a spirit of disinterested research, but with a practical end in view.

For these reasons what follows will be highly selective, very far from complete, and concerned with one or two of the major varieties of habitat only. One word of caution is perhaps advisable at the outset. It is possible that an impression has been given up to now that the ties linking animals in a community are so many and so varied that the interested observer may expect to find furious and unceasing activity, various kinds of animal continually devouring various other kinds, fighting, mating, exploiting one another, coming continually in contact in all sorts of ways. Nothing of the kind. There is no bustle, no hectic hurry in the life of animals. That is a human disease. The life-span of almost all of them is far shorter than that of human beings, but the brevity of life does not worry them. There is plenty of time. There is also, except on rare occasions, plenty of room. They go about their business deliberately, without fuss, and their patience is inexhaustible. Although we can be sure that they are engaged on some occupation, it will seem that many, as we watch them, are doing nothing in particular.

A woodland community

The woodland chosen is the common English oak-wood, with the three layers of growth as previously described. A broad outline of food-chains and niches has been given already, so all that remains is to enter rather further into detail. For this I am deeply indebted to Mr Ernest Neal's *Woodland Ecology*.

Beginning with niches, we find in the first place the three great groups, each one sub-divided. Thus vegetarians in a wood include defoliators such as caterpillars, slugs, snails, mice, and voles; sap-feeders such as aphids, bugs, and frog-hoppers; fruit- and seed-eaters such as weevils, mice and some of the smaller birds; bark-eaters such as bark-beetles, woodlice, millipedes; fungus-eaters such as fly-larvae and some beetles.

Next come the carnivores, predators of many different kinds, ladybird beetles, hover-fly larvae, insectivorous birds, and some preferring molluscs and worms. After them come the mammals, some of them also insect-eaters, foxes, badgers, stoats, hedgehogs. Predators of a different kind are the blood-sucking mosquitoes, as well as parasites such as fleas, ticks, feather-lice. Last come the scavengers of two broad kinds: those that feed on plant detritus in the leaf-litter and the topsoil, such as springtails, earthworms, mites; and those depending on animal matter, the dung-eaters like certain flies and their larvae and many beetles, and the carrion-eaters, again fly-larvae and beetles.

That is a fairly formidable enumeration, but in fact a highly simplified one. The important point is that though keen competition exists between members of the same species, the species occupying the same niche commonly do not compete because they feed at a different time, or make use of what are really different parts of the same niche. Occupiers of different niches do not meet at all.

Food-chains can be divided into three main groups, each division making a separate food-cycle on its own, though with links connecting one with the others. The three can be distinguished according to the plant material on which they are based. First comes the leaves of the trees with the aphids that feed on them, but that one has been described already. The second is based on dead plant remains, on carrion, and on excrement; involving many kinds of insect, woodlice, and spiders, and culminating, like all the food-chains in the wood, in the larger carnivorous birds and mammals. Then there is a very complex cycle involving parasites, many of these including hyper-parasites and so giving examples of the inversion of the pyramid of numbers.

The territorial instinct is much in evidence in a wood, particularly among almost all the birds, both resident and migrant. If there is a sett of badgers it is probable that they regard the whole wood as their territory, of which the boundaries, though not manned, are likely to be marked out by the depositing of scent from their glands. Much the same is probably true for

foxes. Sub-social aggregations will not be lacking, particularly among aphids, the key-industry of the woods, closely packed as they invariably are on leaf and stem. During the winter, hibernating parties of ladybird beetles can sometimes be found under dead leaves. Winter foraging parties of small birds, frequently consisting of more than one species, have been mentioned previously.

I bring this extremely sketchy description of woodland economy to a close with one very striking instance of cooperation. If aphids make up the most important supply of food at the base of food-chains, another almost equally important is provided by caterpillars of many different kinds. These become of special importance to all the smaller birds when they have nestlings to feed. It has been found that there is close synchronization between the requirements, for instance, of parent blue-tits and the time of maximum density of caterpillars of moths of the genus *Tortrix* and others. But cooperation is more finely adjusted than this might suggest, for the growth of nestlings and of caterpillars keep closely in step. As the nestlings become larger and more voracious, so the caterpillars increase in size.

To what extent can this integrated economy be applied to woods of a different kind? In many of them at any rate we can be sure that the parallel is quite close, allowing of course for the contrast in species. In the great coniferous forest belt of the northern hemisphere, for instance, the complex network of relationship could hardly fail to be very much the same. Virtually the same list of niches would serve for both. The species are entirely different, but that does not affect the issue. In an English oak-wood and in the forests of Northern Alberta there are aphids and caterpillars, carnivorous insect-eating birds, raptorial birds. The food-chains connecting them are broadly the same, though some contrast is to be expected from the presence in the Canadian forest of many more large mammals, foxes and badgers in the one, wolves, deer, moose, in the other. As for the equatorial forest, there are added complications, but even there a broad similarity underlies contrasts

brought about, for instance, by the vastly more numerous insect population.

For the sake of completeness this chapter should deal in considerable detail with a great variety of habitats and communities, a number corresponding at least to the great natural regions. This perhaps would be wearisome, even if considerations of space did not forbid it. For these reasons, also because the great continent of animal ecology is as yet only partly explored, I will abandon the land for the rest of this chapter and take to the water, both fresh and salt. After all this is no unreasonable course to take, seeing that salt water alone covers nearly three-quarters of the surface of our planet.

The fresh-water community

We would expect to find niches in fresh water as on land, and again there are the three main types which can be sub-divided. But one contrast between life on land and in the water will be found in the far greater number of animals fixed in one place, at least for their adult stages. The denser medium makes this easy in two different ways: giving buoyancy and enabling them to expand delicate tissues, while at the same time wafting food to their tentacles. On land the nearest approach to a sedentary creature is the spider with her web.

Food-chains, as everywhere else, begin with plants. In fresh water there are in the first place the planktonic algae, including diatoms, in the greatest profusion wherever the current is not too strong to wash them away. Then there are the larger plants, such as the filamentous algae, often seen in floating green scarves, and the higher, rooted, flowering plants – water-lilies, the pondweeds, hornwort, arrow-leaf, Canadian waterweed, and a number of others. To these must be added two floating plants, the carnivorous bladderwort, set with little traps for ensnaring minute animals, and duckweed, both found at times in great profusion. It is important to remember that, except near the bottom of the deeper lakes, photosynthesis is carried on actively in fresh water as well far below as at the surface. Of

all these plants, the filamentous algae provide food for some of the water-beetles, many of the pond-snails, and the tadpoles of frogs, toads, and newts; while the leaves of water-lilies and

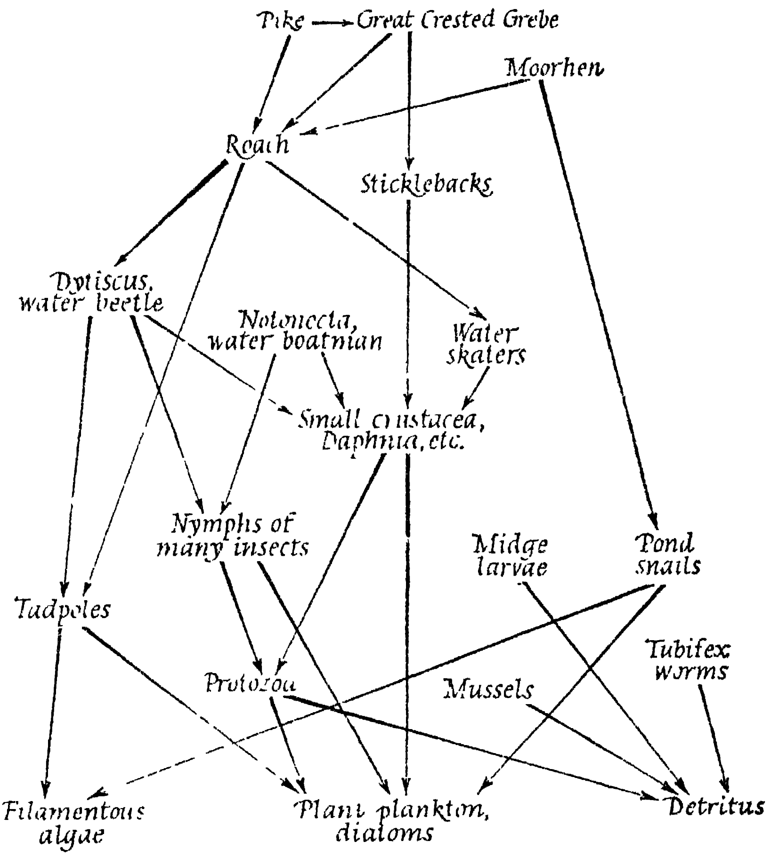

Figure 4 Simplified food-cycle in fresh water.

those of the pondweeds are grazed upon by the larvae of china-mark moths, tucked within their purses of leaf-fragments. The remaining larger plants are of more value as producers of oxygen and providers of shelter and anchorage than as food.

The minute planktonic plants on the other hand are of enormous importance. If anything in the fresh-water community corresponds to the leaves of trees in a forest it is these. There is an almost equally extensive population of animals depending on them. Most important among these are the minute crustaceans *Daphnia*, *Cyclops*, and their kindred, corresponding to the aphids in a wood. The hosts of *Daphnia* in their turn are food for some of the larger water-beetles such as *Dytiscus*, also for the water-boatman, *Notonecta*. These are snapped up by fish such as roach, but some fishes, certainly sticklebacks, by-pass one of these links in the chain by feeding directly on *Daphnia*. At the far end are the major predators, pike on the one hand, and birds such as moorhens and great crested grebes on the other. These two highly simplified examples of food-chains in the two contrasted types of habitat can be expressed diagrammatically thus:

Woodland: Leaves of tree and herb – aphids – ladybird beetles, hover-fly larvae, some small birds – tits, warblers – hawks, owls.

Lake or Pond: Planktonic plants – *Daphnia* – *Dytiscus*, *Notonecta*, sticklebacks – roach, perch – pike, moorhen, great crested grebe.

The third series of food-chains in fresh water is that based on plant and animal detritus collected at the bottom. Many protozoa, some worms, and some of the water-beetles are involved in it, and it corresponds with that based on the leaf-litter and topsoil in a woodland community.

This simplified description, it should be understood, applies only to still waters or to those in which the current is sluggish. In lakes, canals, ponds, and meandering rivers there is a wonderful profusion of life, both plant and animal, provided they are not stagnant and choked with leaves and other dead organic matter. Where the current is swift plant plankton will be swept away, and there will be a corresponding dearth of animal life, except for creatures like the larvae of stone-flies and of some of

the mayflies, both adapted to clinging closely to the underside of stones.

Just as it was possible, where food-chains and niches are concerned, to make an English oak-wood representative of the woods and forests in other parts of the world, so it is with an English pond or river. The species will differ widely, but the general scheme of organization will be similar. Many of the contrasts will occur to anyone, as for instance the presence in African rivers of such enormous vegetarians as hippopotami, or such equally enormous carnivores as crocodiles. In both there will be territories, like those of the stickleback. In both there will be sub-social aggregations like the companies of whirligig-beetles scurrying about on the surface-film, or like fish of various kinds cruising about in shoals.

Communities of the sea

Since, as I have pointed out, life in all probability originated and underwent its earlier development in the great salt waters, it is not surprising that those same waters have continued to provide a habitat for an exceedingly rich animal community. Considered as a whole it is a habitat far larger than any of the natural regions of dry land. Plants higher in the scale than seaweeds have no place there. Insects, rather strangely considering the enormous success with which they have colonized every corner of the continents, have no place there either, with minor exceptions. But algal plants, large and small, and animals of nearly every phylum into which they have been divided, flourish exceedingly.

THE DEEPS OF THE SEA. In the oceanic basins we find a habitat very remarkable in a number of ways. First as to its immensity: more than seventy per cent of the earth's surface is sea, and of this very generous proportion nearly ninety per cent is more than a mile deep. So here we have a habitat many times larger than any in the world; but not only is it extensive, it is also very nearly continuous, not merely with regard to surface

waters but to those above 1,000 metres in depth. Only the Arctic Ocean is separated from all the rest by the Wyville-Thomson Ridge, joining the underwater shelf of Iceland and the Faroe Islands with that of north-western Europe. This means a marked difference in the fauna on each side of the ridge.

In writing of the deep sea one is tempted to make frequent use of the word 'unique'. It would be so easy and so apparently convincing to say that it is unique in a number of different ways, easy but inaccurate. The truth is that where natural habitats are concerned none are truly unique. The word if used has to be hedged about with reservations and exceptions to such an extent as to rob it of its meaning. A qualified uniqueness is no uniqueness at all. A unique habitat would be one ruled by conditions different in kind from those ruling any other. There is no such thing.

This is not a matter of juggling with words. On the contrary it is profoundly important, for it means that the earth as an abode for living things is one. There can be no unique habitat for the reason that underlying biological processes that make life possible are everywhere in their essentials the same. There is diversity to a wide and wonderful extent, but diversity within unity, an extensive differentiation of that which is basically the same. Consider in this way the great deeps of the sea as a habitat, strange, even fantastic. One of its more remarkable features is the relative darkness of much of it, and probably the absolute darkness of a large proportion. At a depth below some 600 metres there is no light that a human eye could detect, a fact of the utmost significance to the creatures that live there, but terrestrial caves also are both relatively and absolutely dark, and are not wanting in animal denizens. Again, below the surface of the sea, pressure increases by one atmosphere for every ten metres of descent. One atmosphere corresponds to a pressure of fifteen pounds to the square inch and is that to which our own bodies are adapted. This increase means that at a depth of miles the pressure is appallingly great, but the difference is one of degree, not of kind, and the creatures that thrive in such pres-

sures are adapted to them in the same way that we are to the pressure of one atmosphere, by maintaining within them the same pressure as exists outside.

The deeps of the sea are also from our point of view very cold. After some 2,500 metres the temperature varies no more than a degree or two above freezing-point. This is cold enough, but a mere nothing compared with some continental temperatures, and it is in this constancy that deep sea conditions come near to being unique. The animals are cold-blooded, like terrestrial creatures other than birds and mammals. Conditions are noteworthy in two other ways. First a general calm, a lack of agitation of the surrounding medium. No motion of waves makes itself felt below about 200 feet, but all the same the stillness is unlikely to be absolute. Some agitation of deep-flowing currents, of which we know little, almost certainly occurs. The other feature is a prevalent low density of animal population. This seems inevitable on account of the relative scarcity of food, and is brought about partly by the sheer immensity of the habitat, partly by the way in which such food as there is becomes available. It seems that over quite extensive areas conditions in this respect approximate to those of the deserts of dry land.

This brings me to the one set of conditions which really do give rise to something markedly different from those in any other habitat, a feature of life in the deep sea more nearly deserving to be called unique than any other. It can be summarized by saying that the animals of the deep sea get their food partly as the result of a slow rain of organic particles from above, like manna from heaven, that process which Rachel Carson in her fine book *The Sea Around Us* imaginatively called 'the long snowfall'. But this is only half the process The rest is a slow rise from the sea-floor up towards the surface of particles equally important though less complex in structure. The snowfall occurs everywhere and all the time, and is a consequence of death, while the rising is periodic, caused by conditions at certain places and some of them at certain times. Nothing quite like this gigantic circulation of food-material occurs anywhere

else, and without it there would be no life either in the deeps or anywhere in the sea. For this reason alone it is worth describing in some detail.

The saltiness of sea-water consists of sodium chloride or common salt and of other salts in smaller proportions, to the extent on the average of thirty-five parts in a thousand. None of these salts plays a part of any importance in the food-cycle. Those which do are other salts, nitrates, and phosphates, present in sea-water in minute traces when a unit of water is concerned, but of huge bulk in the aggregate. They are the same salts as those present in the soil, and like them are liberated through the action of bacteria. Like them too they are necessary constituents of the food of plants. But plants cannot live by these alone. They need the carbon of carbon-dioxide which, as we know, they manufacture by photosynthesis into carbohydrates through the agency of chlorophyll and sunlight. In the sea there is no sunlight except at the surface and for a short distance below. Consequently it is only in the upper layers that plants can live. They are the diatoms and flagellates of the plant-plankton (Plate 6b), frequently and very aptly called the pastures of the sea. It is of course this plant-plankton that forms the basis of all the food-chains in the sea.

But the animals of the abyssal region live far below the limit of plant-life, and as a result can obtain the basis of their food only when the plankton dies and the dead remains, together with waste-products, sink to the depths in the long, unending snowfall. Only a small proportion of these remains will be devoured directly or indirectly as they sink. The rest reaches the sea-floor, where it accumulates in beds and drifts to form the deep-sea oozes. Thus there collects an immense reserve of food-matter consisting of complex organic compounds, and it is on this that the hosts of nitrifying bacteria get to work, just as they do in the soil, rendering it down again into simple nitrates and phosphates. There are no plants at these great depths to make use of this reserve, and as a result, there it would remain locked up and useless if it were not for the other half of the circulation, if it were not for those factors that cause it to rise to

the upper levels, where it becomes available to the pastures of the sea. The sea itself causes this to happen in one or more of a number of ways which are well worth looking into. It is a matter

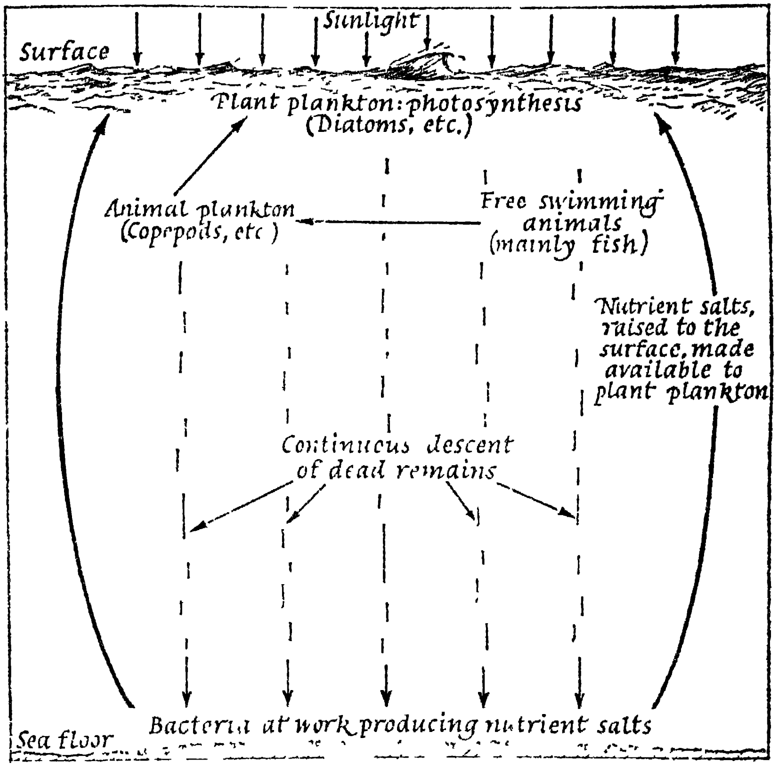

Figure 5. Diagram of food-cycle in the sea.

of temperature and of currents, and there are in the main four of these factors. I was concerned with one of them when describing the reasons for the existence of sea-bird guano on Peruvian offshore islands.

Perhaps the most important of them depends upon the fact that cold water is more dense than warm water, and in consequence tends to sink. This sinking occurs on an enormous scale

round both poles, and as a result forces slightly warmer water to rise from below to take its place. It is this rising water, coming from the depths and rich in nutrient salts, that causes the astonishing wealth of animal life in Arctic and Antarctic seas. The process is more complicated than that, but the broad effect is as described. Another rising of the waters takes place on each side of the equator. At these latitudes the trade-winds blow perpetually from north-east and south-east, thus driving great currents in a general westerly direction. To compensate for this ceaseless displacement, water from below rises to the surface. A third variation of the same theme takes place where one oceanic current impinges upon another. This causes surface water to be drawn away from the area of contact, so creating a sort of vacuum. The only thing that can fill the vacuum is once again water from below. This is what happens where the Labrador Current, flowing south along the coast of Greenland, comes in contact with the Gulf Stream. The continuous upwelling does much to explain the wealth of the fishing-grounds off Newfoundland. The fourth cause is seasonal. In winter, chilled surface-water, that has become exhausted of nutrient salts on account of the activity of the plant-plankton during the summer, sinks. Its place is taken by water from below, which in this way replenishes the supply of salts.

Everywhere in the great oceans, from the surface to the depths, there occurs this unending circulation, separate from but linked with the horizontal circulation of the great currents. The two together bring replenishment of foodstuffs, renewal of oxygen, reinvigoration in respect of all the necessities of life, to every cubic foot of all the scarcely countable cubic miles of the great salt deep. Nowhere can there be anything approaching stagnation, nowhere in consequence any complete dearth of living things. It is all a habitat with the basic characteristics of habitats elsewhere, but of necessity differing in the relative changelessness of its circumstances.

All the same it would be a mistake to make too much of this constancy. Seasonal changes are confined to the upper layers, but from one part to another of the great depths there must be

some degree of change. In the first place there is that between the vast bulk of the water with its swimming life, the nekton, on the one hand; and the floor, with its fixed and crawling creatures, the benthos, on the other. Then what of the floor itself, varying as it does in some degree with the varying nature of the organic ooze with which it is carpeted? Do these wide areas, mapped with some degree of accuracy by bottom sampling, constitute separate ecological provinces, habitats in their own right? We do not know, but on the whole it seems not, though there is reason to believe that the regions of red clay, the widest of all, are very sparsely inhabited.

It is the adaptations to their conditions of living shown by denizens of the deep sea that is the most interesting thing about them, leading as these do to bizarre, and sometimes to comic, forms. It is not the enormous pressures nor the low temperatures these creatures have to put up with that have led to the most remarkable adaptations, since these are essentially the same as those on land. But with respect to absence of light, and to what we must assume to be the sparseness of settlement, there are adaptations of fascinating interest. There is also much that is puzzling and imperfectly understood.

Consider first the question of light. As so often, to generalize is to find our generalizations unsupported by evidence. For instance, it seems reasonable that, since darkness increases with depth, as surely it must, the number of creatures with specialized light-producing organs, and there are a great many of such creatures, should also increase with depth. But it appears that this is not true. Most fishes with light organs do not descend below about 2,500 metres. Again, we can come to a provisional and logical conclusion that there should be two general adaptations to conditions of darkness: on the one hand to dispense with eyes altogether, as has been done by many animals that live in caves, on the other to acquire light organs and at the same time well-developed eyes so as to see by the light those organs provide. But nature, as though to confound elucidation of her secrets, frequently seems to eschew simple arrangements such as this. So it is here. Blind animals are not unknown but

are comparatively rare, while there are some, such as an octopus from 3,000 metres, which are blind and yet possess light organs, so that they are in the strange position of being unable to see by the light they give out.

On the other hand an inquirer would be encouraged to find that there are many creatures possessing both well-developed eyes and light organs. This is true of several cephalopods, the group of molluscs that includes octopuses and squids. One of these, only three inches long, exclusive of tentacles, has very large eyes and no fewer than twenty-four light organs. A large group of fishes known as *Stomiatoids* has rows of lights, like the port-holes of a ship, together with well-developed eyes The same inquirer would be disconcerted by the discovery that there are several deep-sea fish with eyes but no light organs. This is true of a salmonid fish, of more than one of the deep-sea eels, and of a fish belonging to an order allied to the perches. It is difficult to say what he would make of one of the eels known as gulpers with a prodigious gape, which has very poorly developed eyes, but carries a light organ at the end of its whip-like tail. A further disconcerting discovery would be that there are quite a large number of fish, some of the hatchet-fishes for instance, with well-developed, even tubular, eyes directed vertically upwards, associated, if that is the word, with light organs directed vertically down.

There is no room for doubt that a great many creatures of the deep sea are provided with light organs of some sort; some with focusing lenses and reflectors. In some of these the light is produced by special cells, capable of being switched on and off at will. In a few examples bacteria are the light-producers, a most interesting case of symbiosis, if we can suppose that the bacteria benefit in any way. To a very limited extent it is possible to classify light organs according to the function they fulfil. Thus the deep-sea angler fish evidently use them as lures for the enticement of prey. Another purpose is concealment, though here it is not a light organ in the usual sense that is used, but a device for emitting a luminous cloud, as is done by some cephalopods and shrimps. In this connexion it is worth remem-

bering that the shallow-water squid ejects a cloud of ink, like the smoke-screen of a destroyer. But a dark cloud would effect no concealment at all in a dark environment, so the very striking device of a luminous cloud has been evolved instead. A third purpose, traceable in some instances, is to enable the male to find its appropriate female, and cases of sexual dimorphism based on the colour or arrangement of lights have been recorded.

But these are specialized devices, and they leave unclassified a large and varied assortment, so large and so varied, that it is impossible to deny that this prevailingly dark environment has brought forth a whole host of creatures living in darkness yet having eyes, not merely efficient but in some cases very highly developed. They may or may not have light organs. We seem in fact to be forced to the conclusion that there must be light of a sort at depths to which no sunlight could conceivably penetrate. What light can this be but that produced as a collective illumination, however feeble, by the animals themselves? If this could be proved what a wonderful example of cooperation it would be.

In conclusion I cannot resist briefly describing a series of really astonishing devices necessitated by that other circumstance of life in the deep sea, the low density of animal settlement, of which one very important consequence is the relative scarcity of food. Because food is hard to come by, it is of the first importance that deep-sea creatures should make the very most of what there is. The most striking adaptations are those that make this possible. One is a distensible stomach as possessed by one of the gulpers, and in particular by the cross-toothed perch, which is no more than four to six inches long. A specimen of this fish was once drawn to the surface in a completely helpless condition because its grotesquely bulging stomach contained a fish considerably bigger than itself. This could have been cited in Chapter 4 as another exception to the rule that animals depend on prey smaller than they are.

Another and entirely different adaptation with the same end in view is the extraordinary jaw-mechanism of many of the

Stomiatoid fishes which makes it possible for them to open their jaws in a grotesquely yawning gape. To achieve this the head and upper jaw are thrown back into the neck, a feat made possible by the fact that the fore end of the backbone is cartilaginous and therefore easily flexible. In addition to this it is curved into an S-bend. Their teeth are so long and needle-pointed that one species at least is incapable of closing its mouth. These *Stomiatoids* must be among the most ferocious carnivores to be found anywhere and their appearance corresponds to their habits. Being no more than a few inches long they are the most ridiculous little goblins imaginable. But the prize for grotesque appearance must go to another *Stomiatoid* of the genus *Malacosteus*, possessing something different and almost horrifying. This fish has jaws drawn to a point, and head and jaws together are about half the length of the whole creature. But its well-nigh unbelievable appearance is chiefly caused by the absence of any floor to its cavernous mouth. The whole of the lower jaw is made up of a framework of slats so that it resembles a deck-chair from which the canvas seat has been ripped away. At first sight it is difficult to imagine not merely what advantage this can give, but how the creature continues to live. It looks like a freak, a monstrosity, something to be put out of its misery with all speed. Second thoughts however point to the openwork jaw as being a most ingenious contrivance for ensuring a lightning-quick snapping up of prey, for by means of it the density of the water, which would slow down the movement of the most quickly operated, normal jaw, here has no such result. Small prey of course would escape with ease through the gaping framework, but *Malacosteus* is not interested in small prey, engulfing creatures almost as big as itself.

7

TIME AND TIDE: I

THE CHANGING HABITAT

There rolls the deep where grew the tree.
O earth what changes hast thou seen!
There where the long street roars, hath been
The stillness of the central sea.

TENNYSON: *In Memoriam*

UP to this stage it is probable that I have given the impression that animal communities live under unchanging conditions for a long period. It is high time that impression was removed, since it is far nearer the truth to say that conditions are always changing. As was pointed out in the first chapter, many of these changes are of a very familiar kind, those that take place in quick succession, predictably, falling well within the span of a human life. The weather, for instance, changes from day to day, not infrequently in our latitudes from hour to hour, and is bound to influence animals in a number of ways. This is true also of the change from day to night and from season to season. These apply to habitats of all kinds but, as we have seen, there are some more subject to change than others. In our country weather-changes are extremely frequent, but as we go nearer the equator they become less frequent, more nearly seasonal, as of course ours are to a considerable extent. In the equatorial belt itself there is scarcely any seasonal change, while on the other hand that from day to night may be pronounced. Day and night changes are important in all terrestrial habitats, but mean nothing in the deep sea. Changes of these three kinds, those brought by the weather, by day and night, by the seasons, are not always separable from one another. Weather changes are partly seasonal. Seasonal changes bring changes of weather. The change from day to night and back again may bring

weather changes also, while within the Arctic and Antarctic Circles day and night are of such length that the changes they bring are at the same time seasonal and diurnal.

Short-term changes

What is the effect of these short-term changes on the complex web of dependence described in the last three chapters? Many of them are obvious enough. Everyone is aware that some animals are nocturnal, others diurnal. But that is too simple a statement, and it is more to the point to say that there is a food-cycle pertaining to daylight hours and a different one pertaining to the night. The change-over is unlikely to be complete in every respect, but all the same it is very marked, and on the whole what happens is that, while the niches are the same, the animals occupying them are for the time being different. The roles enacted in the drama remain unchanged, but the actors are new. But this is not the whole truth, and there are examples of fresh actors emerging at night to play parts unrepresented during the day.

Beyond doubt it is true that the dramas of day and night are more strongly contrasted in deserts than anywhere else, since there the heat of the sun makes life so intolerable that most animals hide away during the daytime in what shade they can find. There are very pronounced contrasts too in the equatorial forest. But this staging of a different performance once every twelve hours can be illustrated once more with reference to an English woodland. The transition can be watched, and is in its own way dramatic. Just before sunset full daylight activity is still going on. Birds are feeding, singing, courting, but gradually all this dies away as they prepare to roost. The same is true of many of the insects, though here the change-over concerns more species. The only birds active at twilight and afterwards are owls and nightjars, but there is a host of daytime insects – butterflies, beetles, bees, and wasps – and something of a corresponding host of nocturnal ones, such as moths, midges, and mosquitos. The daytime birds catch daytime butterflies

and beetles, and at night it is bats and nightjars that hawk for the insects emerging as dusk deepens. The hawking for moths and minute flying insects by bats is more widespread than any snapping-up of butterflies by tits and warblers during the day. Many other distinctions make themselves felt. In the daytime weasels pursue voles; at night this gives way to a pursuit of wood-mice by tawny owls and badgers. In fact the last two become the major predators at the far end of food-chains, whereas this part was played during the day, in all probability, by sparrow-hawks.

These changes, as well as many others, serve to remind us that the food-cycle is by no means a rigid, unalterable structure; that the web is flexible, and that food-chains become modified. Because conditions are continually changing, the whole complex system of restrictions on competition, of niches and associations of various kinds, must adapt itself accordingly. This form of adaptation is even more marked where the seasons are concerned, when the marked changes that take place between summer and winter are brought about to a great extent by the drop in temperature, though other factors, such as the lengthening period of darkness and a corresponding reduction of light-intensity, play their part as well. In our ignorance as to the exact working out of these changes on the life-processes of animals, we take refuge in the statement that during the winter all animals, though in very varying degrees, find that they must slow down the tempo of their lives, to the extent that activities usual during the warmer months become possible no longer. Naturally this applies to those parts of the world, the higher latitudes, where seasonal contrasts are most marked.

In our English oak-wood the contrast between summer and winter and the transitions between these extremes represented by spring and autumn are very marked, and superficially at least familiar. Insects and molluscs are more profoundly affected than higher forms, so much so that a careful search is needed to find them at all in winter. Snails hibernate, often in considerable gatherings, wherever they can find cover. Insects do the same, but in various stages of their metamorphosis. The

great hosts of aphids over-winter as eggs, as do a large number of other insects, but some do so in the larval or in the pupal stage, a few as adults. As for birds, only the residents, and perhaps a few winter visitors, will be found. Again there occurs a modification of food-chains. Woodpeckers and tree-creepers remain faithful to an insect diet, and no doubt suffer from the scarcity of insects. But they are compensated by adaptations of structure, making it possible for them to find hibernating forms. Many of the other birds are more adaptable to conditions of stringency, exploiting a greater variety of foods than they do in the summer. Mammals in many instances are forced into hibernation, but this, among badgers and bats for instance, may be a partial hibernation only. Once again it is worth remembering that daily as well as seasonal modifications such as these will be found in other forested regions of the temperate zone. Because of the far greater extremes involved, the seasonal contrast in the coniferous forest belt will be that much more pronounced, but statements made concerning an English oak-wood will apply in the broader sense equally well in those vaster woods.

THE SEA-SHORE. One more of these short-term, familiar changes must be given a place here. It is one that applies to a highly specialized habitat only, the sea-shore, and the change of course is that caused by the tide, regular, rhythmical, but varying again rhythmically in the degree of change that it brings about. For the student of animal life it is one of the most interesting of all habitats, and this for more than one reason. Considered historically it has a special claim on our attention, for in all probability it was here, perhaps in a number of places, and on sea-shores that have long ceased to exist as such, that life itself was born. In this connexion we can point to certain qualifications possessed by a shore environment fitting it for its role as the mother of life. It is a matter of light conditions to some extent, also of the circulation and renewal of waters, but most of all of the presence of a high proportion of oxygen in solution. The water of the sea-shore is shallow, with a wide

Plate 1a Hill-country with equatorial forest in Ghana

Plate 1b Savanna grassland, Northern Territory, Ghana.

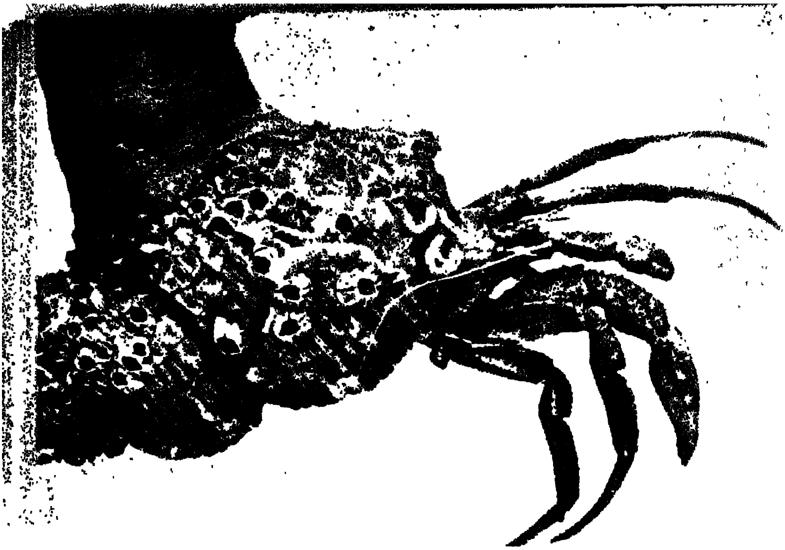

Plate 2a. Multiple commensalism: hermit-crab (*Eupagurus bernhardus*) inhabiting shell of whelk, which carries two sea-anemones (*Calliactis parasitica*), acorn barnacles, serpulid tubeworms (*Pomatoceros triqueter*), and probably hydroids as well

Plate 2b. *Carchesium*, a colonial protozoan (highly magnified). The individual bells are all attached to a single branching stem.

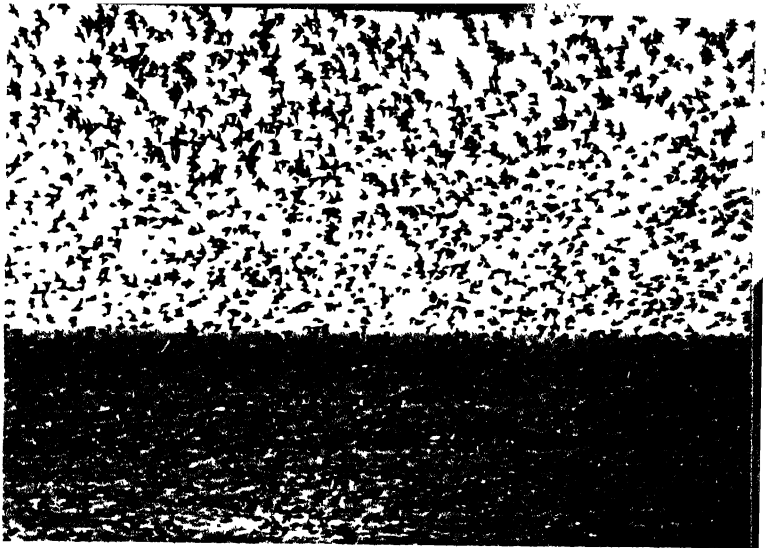

Plate 7a Knots on migration

Plate 7b Breeding colony of guillemots on the Pinnacles, Farne Islan

Plate 4a. Nest of wood ants (*Formica rufa*) in mixed woodland

Plate 4b Fossil forest, Lulworth Cove, Dorset, with silicified boles of cycads of the Jurassic Period

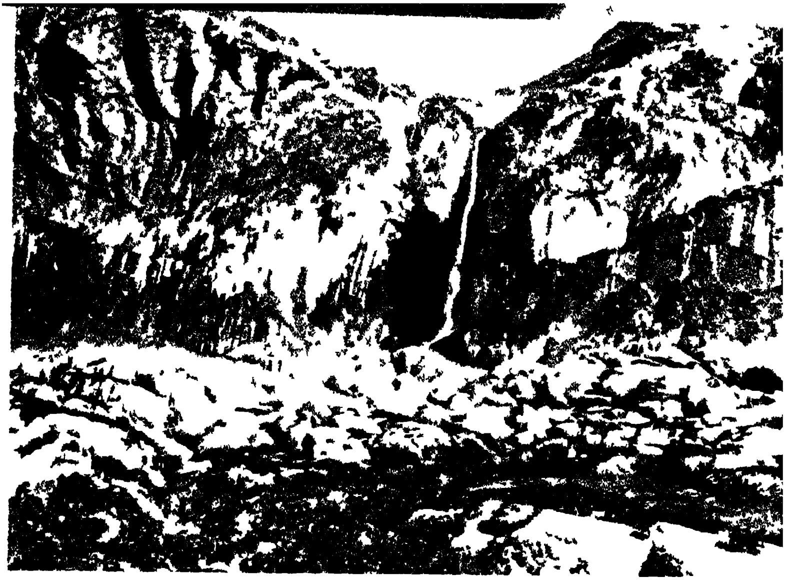

Plate 5a Rocky coast in Pembrokeshire. The *Pelvetia* seaweed zone appears in the foreground, with the zone of lichens above

Plate 5b Molluscs of the splash zone, exposed in cracks of rock above high water mark. *Littorina rudis* and *L. neritoides* (smaller)

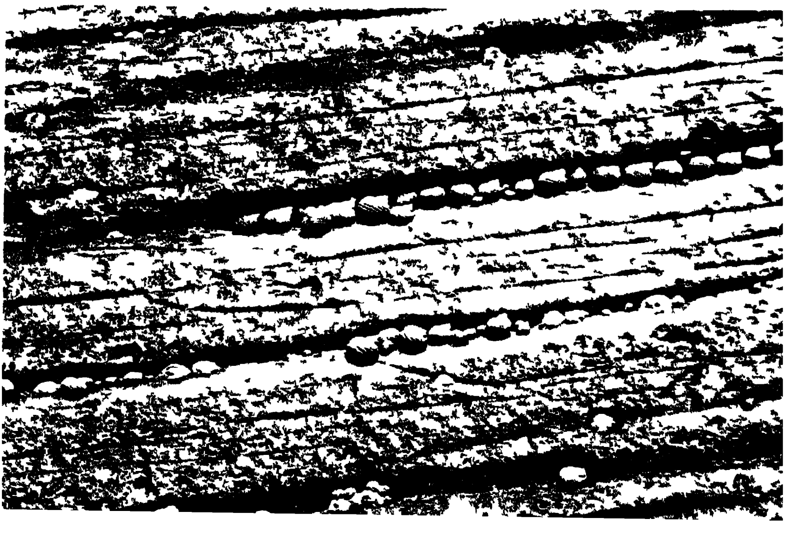

Plate 6a Courtship of small tortoiseshell butterflies. The male approaches the female from behind and caresses her body with his antennae

Plate 6b Plant plankton of the sea (highly magnified) Diatoms (chains) and flagellates, also a copepod (animal plankton

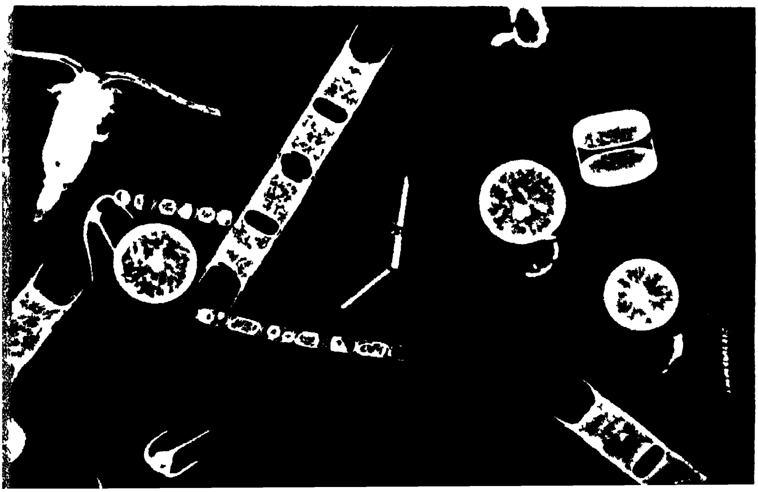

Plate 7a Male great crested grebe with chick Soon after hatching, chicks of the great crested grebe are fed on feathers plucked from the breast of the parent, as seen here The young are carried on the backs of the parents for about two weeks

Plate 7b Golden plover watching chick This is one of those birds whose young leave the nest almost immediately after hatching

Plate 8. Cock blackcap feeding young. The chicks remain in the nest for several days.

Plate 9 Scottish crossbills. Courtship feeding. The cock feeds the hen while she is on the nest. Often this is done ceremonially away from the nest, as a part of the ritual of courtship.

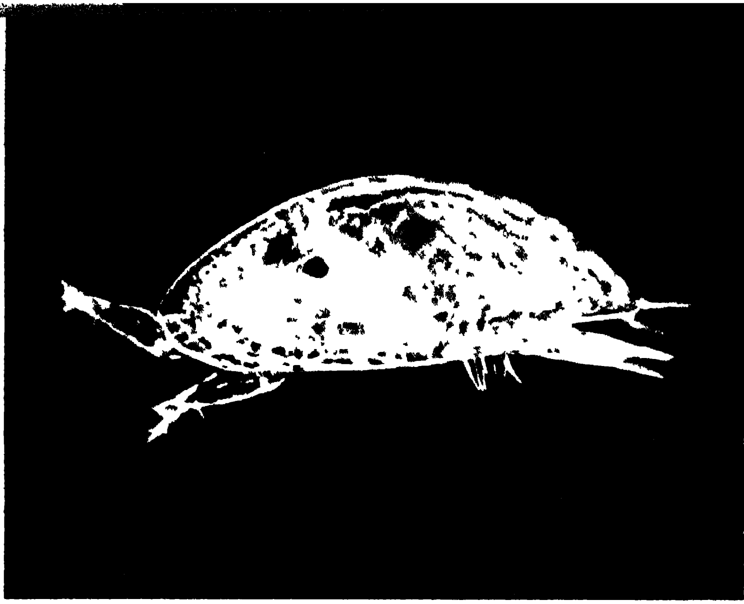

Plate 10a. Cypris larva of acorn barnacle (highly magnified) This is the free phase of development, before the creature becomes attached to a rock

Plate 10b. Acorn barnacles exposed on rock This is the fixed, adult phase, with opercular plates closed

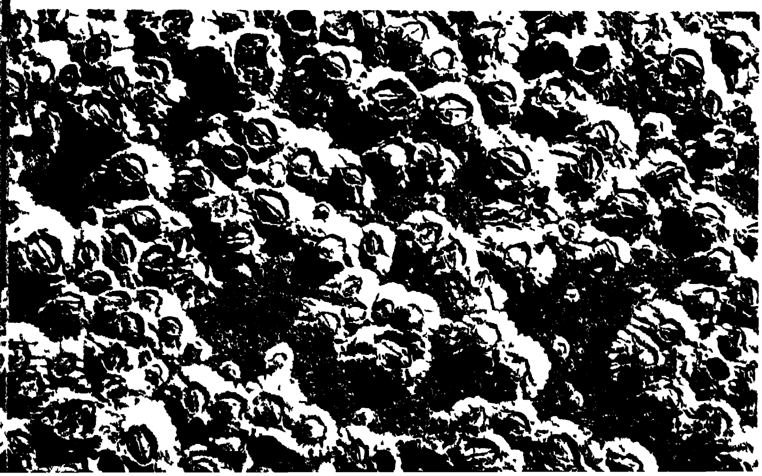

Plate 11a Clifden nonpareil moth, *Catocala fraxini*, with wings closed *Plate 11b* Wings spread, black and lilac coloration of hindwings exposed

Plate 12a. Grey dagger moth (*Apatele psi*), almost merging with a lichen-covered tree-trunk

Plate 12b Batesian mimicry hornet moth (*Sesia apiformis*), a clear-winged moth closely resembling a hornet

Plate 12c Wasp beetle (*Clyteus arietus*). Probably this is a member of a Mullerian association

Plate 12d Protective resemblance larva of grey pine carpet moth (*Thera obeliscata*) on food plant.

exposure to the air in proportion to depth. As well as this it is in a state of constant agitation, and both of these are conditions giving rise to liberal oxygenation. Moving water always contains more oxygen than still water, a swiftly flowing stream for instance as opposed to a sluggish one.

Another reason for the peculiar interest attaching to the sea-shore, and one that means more to us here, is its dual nature. So far we have considered aquatic habitats and terrestrial habitats, but the sea-shore fulfils both conditions, is at one time aquatic, at another terrestrial. The transition from the one to the other takes place in rapid succession, on the average four times during the twenty-four hours; every stretch of this far-flung zone having two phases of high tide and two phases of low tide every day. For the first time we must bring the moon into the ecological picture. Once every fortnight the sun and the moon exercise their gravitational pull in the same direction and the tide advances farther and retreats farther. These are the spring tides. During intervening fortnights sun and moon are pulling at right angles and the tides are less pronounced.

In no other habitat does this change from the aquatic to the terrestrial occur, and the sea-shore is to that extent unique. Naturally it is of enormous significance for all its denizens both plant and animal, which are required to adapt themselves, some to exposure for a short period only, others to a much longer one. The peculiar interest of marine ecology lies in the extent and the nature of these adaptations. The situation can be summed up to this extent: when the sea covers them the animals of the sea-shore can lead what we may call their normal existence, governed by the food-cycle already described, swimming or crawling if they are mobile creatures, waiting for food to be wafted to them if they are sedentary. For the rest of the time their environment becomes a terrestrial one, all activity has to cease, while they lie hidden and expectant for the turn of the tide. During this phase too, creatures of the neighbouring land-mass, breathers of free oxygen, seize the opportunity to reap a harvest from these waiting ones. They are almost entirely birds,

waders such as oystercatchers, dunlins, and the rest, often in great flocks on a sandy or a muddy shore; rock-pipits, gulls, turnstones on a rocky one.

That is a generalized statement covering a multitude of adaptations. The fundamental problem for sea-shore animals is to seek out a cranny, either around or within them, where there is moisture and therefore dissolved oxygen sufficient to enable them to survive their spell of waiting. One important device is to enlist the cooperation of plants, the seaweeds that cling in thick draperies, carpets, and curtains, all saturated with moisture. Another, on the same sort of shore, is to withdraw into hollows and cracks which the sea itself has gouged out. Among them the rock-pools retain their water even when the tide has ebbed, and so to become a member of one of these little pellucid worlds of colour and transparency is perhaps the best device of all, since it means that for these creatures – sea-anemones, prawns, various molluscs – conditions remain virtually the same at all states of the tide.

As for crannies within the animals themselves, that is a matter of sealing their moisture-bathed gills from the outside world. This applies chiefly to crustaceans and molluscs and is effected in a number of ways. Some of the molluscs achieve it by means of a lobe covering entrance and exit. In others the branchial chamber is enclosed in a tube or siphon. Limpets press their shells within meticulously corresponding oval depressions carved by their own efforts in the face of the rock, while acorn barnacles isolate themselves for hours at a time by means of four closely-fitting opercular plates. It can be added here that these two very common shore animals are thoroughly adapted to another circumstance of the shore, namely the pounding of great waves. The acorn barnacle achieves immunity by means of a cement, the limpet by a method not clearly understood. All we can say for certain is that the setting up of a vacuum between itself and the rock fails to explain the proverbial steadfastness of its attachment. The small univalve molluscs simply allow themselves to be rolled to and fro without concern.

But perhaps the most striking of all adaptations to conditions of alternating exposure and immersion, the most widely adopted and therefore the most noticeable, is that of horizontal zonation up and down the shore. Broadly speaking this sharing of the habitat is brought about by those creatures most adapted to long periods of exposure taking up their station high up on the shore, while those less adapted confine themselves to lower, more seaward, positions. This means that at one extreme we find creatures inhabiting that far landward zone, covered only by the highest spring tides, and not always even by them. At the opposite extreme are those exposed by the same spring tides, but this time at their farthest ebb.

In this case, as in others, we must begin with plants, the seaweeds, since it is they that arrange themselves most noticeably in zones, while the animals take varying advantage of the cover they provide. The typical formation, beginning at the upper levels and working seawards, consists of five or six well-marked zones. First there should be mentioned one beyond the reach of the highest spring tides, and therefore beyond the reach of the seaweeds. The plants there are certain shore-loving lichens. Below this, belts of seaweed, each of one dominant species, follow one another seawards, though not every stretch of shore will show all of them. The highest consists of tufts of the channelled wrack (*Pelvetia caniculata*) (Plate 5a), which over the period of neap tides, when the sea fails to cover it, may lose up to sixty-five per cent of its moisture, becoming dry, brittle and blackened, to all appearances dead. It has been calculated that the uppermost fringe of this belt is exposed to the air for as much as ninety per cent of the time during each year. The three succeeding belts, each less exposed as the lower limits of the shore are approached, are those occupied by the flat wrack (*Fucus spiralis*), the knotted wrack (*Ascophyllum nodosum*) and another *Fucus*, the serrated wrack (*F. serratus*). This, strictly speaking, is the lowest zone of the shore proper, and is usually fully exposed only by spring tides; but lower still yet another belt generally comes at least partly into view. This is the Laminaria zone, thickly grown with the long, leathery

thongs of tangleweed (*Laminaria digitata*) with its knotted holdfasts.

Clearly these seaweed zones deserve to be called plant communities, exhibiting the principle of dominance to a very marked degree. Because they are plant communities, rather sharply marked off from one another, we would expect them to give shelter to animal communities to some extent corresponding. So they do, but the correspondence is loose, with an overlapping of species from one zone to the next. A broad correspondence cannot fail to show itself, at least to the extent that as we work down the shore, the number and variety of demandingly aquatic creatures will steadily increase. Molluscs show this more clearly than any other large group, and it happens that one kind of mollusc, the periwinkle, members of the genus *Littorina*, are graded up and down the shore in a way that corresponds quite closely.

Far up the shore, above the *Pelvetia* zone, you may frequently come upon rows of tiny molluscs fitted snugly into crevices of rock. This is *Littorina neritoides*, the small periwinkle, with shells not more than a quarter of an inch in diameter, a very unobtrusive creature but a very interesting one. It lives wholly in what is known as the splash-zone, wetted only by spray. In spite of this it appears that we must class it as a marine mollusc, though it is reasonable to think of it as a creature now in process of making its way from sea to land. The small periwinkle is beautifully adapted to its strange half-way existence, for though capable of withstanding a period of exposure of up to forty days, it still depends on the sea for propagating its kind, spawning during the winter months when storms are likely to convert the splash-zone into something more. There is good reason for supposing that spawning periods come at fortnightly intervals, corresponding with high spring tides.

Lower down the shore another periwinkle (*L. rudis*) is found (Plate 5b), a little larger than *neritoides* and with a ribbed shell. These two overlap to some extent, and if *neritoides* is to be looked upon as a marine animal in process of becoming an inhabitant of dry land, the same must be said of *rudis*. It is

extremely interesting and a little puzzling that *rudis*, in spite of the fact that it lives in a habitat more strictly marine, nevertheless has perfected a method of reproduction particularly suited to the land. In both these species fertilization is internal, that is to say the sexual products are not discharged into the sea in the rather remote hope of their meeting. On the contrary the male mounts the female. This gives the advantage of enabling a protective envelope to be formed round the spawn. But *rudis* goes one step farther. It is viviparous, which means that the young do not leave the body of the mother as fertilized eggs, but as well-developed infants complete with shells. They immediately set about the business of populating the shore. *Neritoides*, though penetrating farther from the sea, is yet dependent on it for disseminating its extruded eggs.

A third member of this genus, the flat periwinkle (*L. obtusata*), is most commonly found among the fronds of *Fucus spiralis*. Most of them are bright yellow, but they may also be brown, black, olive-green or striped. Last of these periwinkles comes the common winkle of seaside stalls (*L. littorea*), ranging more widely than the others, covering more than one zone. These last two periwinkles then are almost wholly aquatic. It is of the utmost significance and interest that the two pairs of species differ from one another structurally as well as in respect of their habitats. The two aquatic species, *obtusata* and *littorea*, have gills of the kind normal to aquatic animals; while the other two, both so to speak on their way to the land, possess a breathing apparatus much more like a lung, of the type found in the garden snail.

On sandy shores conditions are wholly different. There is no seaweed and no rock-pools, nor is there any need for them from the point of view of animals inhabiting such shores. Their problem is to protect themselves from the impact of breakers, and all they have to do is to burrow into the sand which is their sure refuge, not only from breakers but from the danger of desiccation and of oxygen-scarcity as well. For sand, provided it is not too coarse, holds water like a sponge, each particle surrounding itself with a film of water, just as with soil on the

land. The sand of the sea-shore in fact is a thoroughly satisfactory medium for life, so long as the animals concerned have possessed themselves of the necessary adaptations. In addition to giving protection from the two major dangers of life in the inter-tidal zone, the sand is a rich source of food if properly exploited, and shields its inhabitants from alternations of temperature and from reduction in salinity likely to occur near the mouths of rivers. Changes of these two kinds are confined to the surface layer.

Animals belonging to many of the main phyla have discovered this refuge – worms, a few crustaceans, one remarkable sea-urchin, and a number of molluscs. Nothing like the variety of species characteristic of rocky shores can be expected. On the other hand the numbers of some of them, such as lugworms and cockles, are often enormous. It is the quest for food in a medium necessarily less rich than sea-water itself, that gives rise to interesting adaptations. One way is to filter food out of the water above the sand by means of siphons, as is done by cockles. Another is to collect it from deposits of plant and animal detritus on the surface of the sand, also by siphons. These two methods can be used only at flood-tide. A third method, that adopted by the lugworm, is to swallow sand in great quantities, extracting whatever food it may contain. The casts of the lugworm, piled in little heaps over the 'ribbed sea-sand', are as familiar as those of the earthworm on a lawn, and these two well-known worms provide an excellent example of animals occupying the same niche in wholly different habitats, niches that include living-conditions as well as method of feeding. A fourth niche filled by these sand-dwellers is that of those who prey on the rest, the carnivores, mainly fish.

The sea-shore is a habitat so crowded with life, providing so many examples of associations already referred to – niches, food-chains, parasitism, commensalism, symbiosis, protective resemblance – that many more pages could be covered describing it. But space is limited and I must confine myself to two more points. One concerns the niches of two of the commonest animals of this habitat. The limpet and the acorn barnacle are

found together, often side by side, and at times sharing the same restricted habitat so intimately that acorn barnacles not uncommonly take up their fixed abodes on the shells of living limpets. Yet the two in no way compete, for while the acorn barnacle is a plankton-feeder depending on its food being wafted to it, and assisting the process by the combing and grasping action of twelve feathered feelers which structurally are legs, the limpet is a peregrinating grazer, exploiting the filmy algal growth over a territory within a radius of a few inches from its base. When about to be abandoned by the tide, it makes for its own exclusive anchorage and finds it unerringly by what can only be called a homing instinct as yet unexplained. The barnacles then have no reason to resent the presence of limpets; far from it since the limpets, by their grazing, clear rock-surfaces of their film of vegetation, and so provide ground better suited for the permanent residence of barnacles.

Finally some indication of the enormous density of some shore animals must be given. It has been estimated, for instance, that over a stretch of shore about a mile in length, the lugworm population can be as high as three to four million. A square foot of rock can provide homes for well over 2,000 acorn barnacles, while if an estimate is made over a stretch again about a mile in length, it may well reach the staggering figure of about a thousand million. With figures such as these it seems futile to talk of overcrowding, but it would be interesting to know what is the optimum density of lugworms or acorn barnacles, and still more interesting to know what benefit, if any, they derive from being associated in such astronomical numbers.

Plant succession

The vicissitudes of time with which this chapter is concerned clearly fall into the two groups of small and large, short-term and long-term, but perhaps that is rather a crude point of view. Better to think of them as parts of a whole, even if what I have called a whole amounts to the entire past of this planet, if not to eternity itself. Looked at in this way they fall into their

places in the scheme of things. Just as minutes are components of an hour, hours of days, days of months, and so on, so in ecology the lapses of time of the short-term order, such as day and night, tidal rhythms, the seasons, are components of another kind of change having a larger amplitude, the kind known as plant succession, giving rise in time to the vegetation of the great natural regions. Plant succession as a change falls far short, in its turn, of yet others with the largest amplitude of all.

I have referred briefly to this process in Chapter 2, but it now needs more detailed examination. Stated simply it is the process by which an initially bare surface becomes covered gradually and in stages into one closely settled by plants. The final result, as I have said, is known as the climax, consisting of that type of vegetation which the climate of that part of the world is capable of supporting. The whole cycle, beginning with a bare surface and ending with the climax, is known as a sere. What this means is that plant communities are far from being stable, that they develop from one stage to the next, and that the change is brought about mainly by the plants themselves. It is very largely a matter of the deposition of humus. The earliest arrivals are lichens and mosses, and these in the fulfilment of their lives, including the formation of humus, gradually change the conditions of the habitat so that it becomes suited to plants of a different and more highly developed kind. During these early stages the plant community is of the kind known as open, spaced out, but as more and more spores and seeds arrive, carried by the wind or deposited by birds, the bare spaces are filled up and the community becomes steadily more dense, of the kind known as closed. Herbaceous plants, following the pioneers, and tending to suppress or drive them out altogether, lead to a further accumulation of humus, until conditions favourable to shrubs are set up. This may be the climax. On the other hand the climate may favour the growth of trees, in which case the climax will be forest.

Plants then tend to drive each other out until the climax is reached, and that climax, whatever it may be, will remain stable

at least for a while. A sere often begins on bare rock which is a dry surface, but it could just as easily begin on a very wet one, such as silt deposited by a river, or a shoal of sand by the sea. An important consequence of the colonization of these two extreme kinds of initial surface is that a dry one, by the deposition of humus, tends slowly to become less dry. Conversely a wet surface tends to become less wet, again because of the humus being constantly laid down, with the result that the level is gradually raised. This is what happens on the edges of ponds and lakes which, by the action of the plants that take root there, are continuously in process of becoming silted up. This tendency of dry areas to become wet and wet areas to become dry means a slow progression, wherever plants can grow, towards an intermediate condition, neither very wet nor very dry. The process is never-ending, since there are always agencies at work to provide on the one hand flooded regions and on the other dry ones, on each of which the cycle begins afresh. A river changing its course will give rise to both kinds of surface but in different places. The sea may advance here and retreat there. A very notable agency, producing wide stretches of bare and arid land, is volcanic activity, whether of the comparatively gradual kind, building great plateaux of lava, or explosive eruptions scattering prodigious quantities of rock-dust and perhaps blasting a whole countryside out of recognition.

Volcanic activity is comparatively rare and localized in terms of human life, or even of human history, but in terms of earth-history it must be reckoned as a common occurrence, something that happened at one time or another over the whole earth. One very famous eruption made it possible for the establishment of a plant sere to be closely observed. This was when in 1883 the island of Krakatoa was almost destroyed in a series of stupendous explosions. The island is, or was, in the Strait of Sunda, between Java and Sumatra, and the eruptions blotted out all traces of life on what was left of the island. Later it was visited by scientists three times. At the first visit, in 1886, it was found that the rock was becoming colonized by algae, mosses and ferns, the spores of which must have been carried by the wind.

Along the shore seeds and fruits of flowering plants had been deposited by ocean currents and some had germinated. A few had begun to spread inland, where a few grasses had taken root as well. By 1897 more than sixty species of flowering plant had managed to establish themselves, while in 1906 it was found that the whole island was covered by a closed community of vegetation.

As an example of a sere of the other kind, beginning with a moist area, I may cite the development of a saltmarsh through the action of the sea along a low-lying shore. It begins with the laying down of silt forming a flat of varying extent. This too has a feature of special interest because we find plant succession, which is a change of a comparatively long-term kind, working in cooperation with one of the short-term changes. For we must bring the tide into this, since the stretch of silt in question will be exposed at one state of the tide, covered at the other. Each high tide leaves behind a film of silt, so that before long a typical salt-loving plant, such as *Salicornia*, or saltwort, will begin to colonize it. The roots cannot fail to hold up the flow of water and so stimulate the accumulation of silt. This goes on, the level gradually rising until the more inland stretches are no longer covered by the tide. Then a kind of grass, *Glyceria maritima*, gains entry and helps to stabilize the developing soil with its fibrous roots. The level continues to rise and another grass, *Festuca*, joins the community. Meanwhile rain does much to wash away the salt, and the marsh in time ceases to be a marsh. Other plants such as rushes come in, so that after a further interval what was once oozy, salt mire becomes something approximating to a heath.

I hope it is clear to what this rather long dissertation on plant succession is leading. Plant communities are continuously changing. Animal communities are intimately, though not quite correspondingly, linked to plant communities. It follows therefore that plant succession involves some sort of animal succession, that animal communities also inevitably undergo slow, continuous change. Now animal succession is a more complicated affair than plant succession, partly because of the rather

loose association of animals with plants, partly because they depend on different factors for their welfare and their dispersal from place to place. Also they tend to hang on in many cases longer than plants, some contriving to adapt themselves to changing conditions. For these reasons it is difficult, if not impossible, to predict the course of animal succession.

In the island of Krakatoa it was a matter of the gradual restoration of the *status quo*, that of the fauna of an island separated from neighbouring islands, almost large enough to be called land-masses, by twenty miles or more of sea. The first colonists would be insects of kinds small enough to be carried by the wind, together with spiders. Then would come larger insects such as butterflies, conveyed thither not necessarily willy-nilly on the wind, but perhaps migrating under the influence of some urgent compulsion, their survival depending on their success in finding appropriate food plants for their larvae. With them would come birds, depending on the insects for subsistence, or on the fruit and seed of plants. The birds would help in the spread of plants by depositing seeds eaten elsewhere, and it is possible that some of these would be the seeds of plants needed by the larvae of insects, or by the birds themselves. Not impossibly other animals, such as reptiles or even small mammals, could be carried on drift vood.

As for the saltmarsh, there would be no *status quo* in the same sense to be restored, but the setting up of a new land-surface won from the sea. The animal succession would be more truly a succession, beginning with a marine fauna adapted to life in mud, a varied population of worms, including one of the ragworms, and perhaps a colony of the beautiful peacock-worm with its feathery corona of tentacles. There would be molluscs in considerable variety including cockles, and mud-burrowing amphipod crustaceans. Gradually these creatures would find life impossible as the level rose above the influence of the tide. They would perish or migrate seawards, and their place would be taken by others favouring a terrestrial environment, notably insects, accompanied by birds such as geese and redshanks. In time a heathland community would be set up with a great

variety of insects and spiders, together with birds such as stonechats, meadow-pipits, and stone-curlew. There would certainly be rabbits, myxomatosis apart, and this is worth mentioning because these prolific creatures by their incessant nibbling often prevent a plant succession from reaching its climax. What without them might well develop into shrubby growth, or even woodland, remains in what is known as a sub-climax condition of heath or grassland. Much the same is true of deer, and still more so of sheep and cattle. Man indeed, with his varied and far-reaching activities, can hardly be left out. Obviously in any closely settled country human activities in pastoral farming, the clearing of woodlands, to say nothing of crop-growing and the sheer blotting out of natural environments by building, is by far the most influential of all factors where plant succession is concerned.

Long-term changes

It is clear that the influence of plant succession is enormously important because of the inevitable changes in animal life that it brings about. It is important for another reason, since in the widest sense it has caused the surface of the earth to be divided into those great natural regions which are vegetation belts determined by climate, and at the same time provide habitats for animal communities of the broadest extent that we can recognize. Because of the shortness of the span of human life, we look upon these natural regions as fixed and unalterable. In fact they are far otherwise, as the history of the earth teaches us. This brings me to those changes having the greatest amplitude of all, and to the rather unexpected statement that because the natural regions are continually, if from our point of view very slowly, on the move, advancing in one place, retreating in another, the animal communities associated with them advance or retreat at the same time. A migrating plant community inevitably carries its animal inhabitants with it as it goes.

Evidence for these great changes from one set of conditions to another, differing from it in almost every way, lies all about

us, if only we know where to look and possess the knowledge to interpret what we see. We need go no farther afield than these islands to find it in abundance. To take one localized example, on the coast of Dorset, a few hundred yards to the east of Lulworth Cove, there is a so-called fossil-forest (Plate 4b). Most fossil-forests are found on the shore, exposed only at low tide, giving clear evidence of the submergence of a former coastline, but this one has been raised some fifty feet above the sea, and now occupies a wide ledge littered with angular boulders of limestone, white, arid, and glaring in the sun. Among the tumbled rocks are the silicified boles or stumps of trees, each with a cup-shaped depression in the middle. They are all that is left of cycads, a kind of primitive cone-bearing tree, still found in other parts of the world. There are one or two prostrate trunks as well, they and the boles petrified, their true nature betrayed only by their shape. In Jurassic times, some 150 million years ago, a forest grew here, though not at its present level. You can see to this day, running irregularly over the ledge near the bases of the stumps, a strip of dark gravelly earth less than a foot in thickness. This is the highly compressed and contorted remnant of the soil, a fossilized land-surface, in which the cycads once grew.

What sort of animal community once lived and moved among these immemorial trees? We have little but moderately informed surmise with which to answer. Insects most certainly, for they come of a very ancient stock. Perhaps some of the earliest birds, not unlike that very nearly unique fossil *Archaeopteryx*, found in Bavaria, fluttered weakly among the stiff, palm-like foliage. There may even have been a dinosaur or two, only a few of which had the sensational dimensions of *Brontosaurus*. Today animals are little in evidence – springtails wandering inconspicuously, beetles lurking under the rocks, an occasional butterfly, skylarks far above, and the gliding, ironically laughing herring-gulls.

Go to a district on the outskirts of Oxford, recently built up with rows of highly desirable small residences, complete with sanitation, refrigerators, and television sets. Out of the midst of

this select and up-to-date neighbourhood rise low wooded heights, as yet spared from the curse of development. Villas, tarmac roads, back gardens, garages, as well as the wooded heights, are all founded on a sub-stratum of coral, and the whole district was once a reef barely awash in a warm tropical sea. Possibly the *Plesiosaurus* swam in those long-vanished waters, and it is not unlikely that one of the pterodactyls, perhaps *Pteranodon* with its twenty-seven-foot wing-span, glided low over the waves. It is improbable that the people living in those houses today give much thought to their predecessors.

Then there are the coal-measures of the north and of South Wales, where great humid forests of the Carboniferous Age, nearly 300 million years ago, flourished exceedingly in a climate not unlike that of the equatorial belt at the present time. If the climate was similar, the trees were wholly different, for this was the age of the giant horsetails, club-mosses equally tall, the strange scale-tree, *Lepidodendron*, seed-ferns, and primitive conifers. Early amphibians swam and splashed in great lagoons of standing water. There flashed dragonflies with a wing-span of two feet, the largest insect that has ever existed.

But of all the multitudinous changes of the remote past, those that mean most to us today, because most recent, are the ones caused by the Ice Age. It lasted in all for about a million years, and the age in itself saw wide and varied changes, for though we speak of the Ice Age, it is now known that there were four periods of glaciation, with much warmer inter-glacial stages between. The Pleistocene Ice Age ended about 25,000 years ago; this of course is little more than the day before yesterday in the geological scale of time. It seems clear from the moraines and other traces left behind so recently that, at least in the Alps and perhaps here in Britain, there were these four stages of the onset of cold conditions, together with the intervening stages of retreat, and there is little doubt that there were corresponding retreats and advances of communities of plants with their associated animals. Of the comparative severity of each of the stages of glaciation we know something in broad outline, and it is clear that each advance of the glaciers must in a manner have

pushed before it a wide belt of country in which conditions were like those of the present high Arctic tundra, a partially closed association of mosses and lichens, with precious little else in the way of either plants or animals, at any rate for the great part of the year. At a considerable distance beyond the reach of the advancing glaciers, conditions must have remained somewhat easier for a time. There would be shrub communities, and farther yet, the one merging into the other, birch-forests, pine-forests, and even oak-forests farthest of all. Each of these would have a comparatively dense settlement of animals.

But all these belts were inevitably doomed and at each peak of glaciation vanished entirely, at any rate north of a line roughly corresponding to the present course of the Thames, though there is disagreement as to the extent to which plants and animals were wiped out or retreated south of what is now the English Channel, which at that time did not exist. Then after some thousands of years the engine of glaciation went into reverse, the ice-sheets retreated, the vegetation belts advanced as it were in pursuit, carrying their animal communities with them. During the first half of the Ice Age as a whole our fauna was an exceedingly rich one, with such exotic creatures as elephants, sabre-toothed tigers, the woolly rhinoceros, bears, wild pigs, deer of many sorts, as well as a host of small rodents. It seems likely that all of these were driven south of what is now Britain during the second cold phase which appears to have been the most severe of all, and this probably means that some at least returned when conditions improved.

The whole story is extremely complex, but it is clear that during what we suppose was the final retreat, plants and animals slowly returned, those that is to say that had not in the meantime become extinct. This went on until, some 7,000 years ago, the way was barred and Britain became an island. Apart from that notable change there were others covering the period between the end of the Ice Age and the present. These were changes of climate, alternating phases of warm, dry conditions with others equally warm but with a heavier rainfall. These alternations are known to us from recent methods of sorting out

and identifying pollen-grains found in deposits of peat at various levels. This technique of pollen-analysis shows what kinds of tree were dominant at various times, and from that the climate can be deduced. It follows that animal communities must have alternated to a considerable extent correspondingly.

8

TIME AND TIDE: 2

THE CHANGING ANIMAL

There is grandeur in this view of life . . . that whilst this planet has gone cycling on according to the law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

CHARLES DARWIN: *The Origin of Species*

THE changing environment is one thing and of the greatest importance, but is far from being the only kind of change to be taken into account. It has a direct connexion with that other infinitely varied series of changes which has resulted in the wonderful diversity of animals that we know today, to say nothing of a host of creatures that have vanished from the face of the earth. My concern now is with this kind of change, with evolution in so far as ecology enters into it; and that, it must be made clear at the start, is very far indeed. For many years the intimate connexion between the two was not recognized. From the time of Darwin until comparatively recently, while a flood of light was thrown on the manner in which animals have evolved, their evolution was considered almost solely according to their anatomy, or their outward appearance, as though they had existed in a sort of vacuum, unaffected by their surroundings. But that is a thing of the past, and it is now fully realized that the study of evolution must go hand in hand with the study of ecology. Fossils, for instance, can tell us much concerning the evolution of living organisms, but after all it is the environment that has become fossilized as well as the creature itself, and the one is as significant as the other.

This is not the place to embark on a detailed dissertation of all that is involved in evolution, even if I were competent to do

so, but some brief explanation is perhaps called for. It can be reduced to simple terms by saying that evolution depends in the main on two things: first, inherited variations, that is to say, differences between members of the same species, contained, so to speak, within the animal itself; and secondly on natural selection, which tends to eliminate disadvantageous variations and perpetuate those that confer an advantage in the battle of life. It should be clear that of these two the first is internal, has no connexion, or perhaps it had better be said no known connexion, with the habitat in which the animal lives. The second on the other hand has every connexion. But that is an understatement, and it could be said that natural selection can be defined as the influence of the environment on the animal living in it, whether that is a matter of climate, of soil, of plants, or of the other animals in the community.

One vitally important point must be stressed and it is this: the environment is quite capable of acting on one individual of a species so as to cause it to differ from other members of the same species. That is an acquired variation, but it is not the kind of variation that evolution is concerned with, because such a variation cannot be inherited. It is only heritable variations that matter, those capable of being handed on from parent to offspring. It is these inherited variations that are the raw material of evolution.

A word as to the manner in which inherited variations appear. Most animal bodies are made up of countless millions of cells, though, of course, there are unicellular animals, the protozoa, possessing one cell only. Most cells contain a nucleus, and every nucleus contains a number of thread-like bodies called chromosomes, of which there is a fixed number for every species, though this must not be taken to mean that each species has a different number. Each chromosome contains a large number of units known as genes, which are responsible for the various features or characters of an organism, whether plant or animal. It is the handing on of genes in the nuclei of the germ cells, eggs or sperms, that explains the close similarity between parents and offspring.

Our concern is with variations between one animal and another, and these can take place in two ways. First, in the course of the pairing and division of chromosomes taking place in the nucleus, it is possible for them to break and reunite somewhat differently, or for part of a chromosome to change places with the corresponding part of another chromosome. Such movements may lead to a re-combination or re-shuffling of characters, and these could cause variations, but to a limited extent only, since they could mean no more than some re-assortment of characters already present. Much more important is a change in the nature of a gene, and if this takes place in one of the germ cells then the change will be handed on to the next generation.

Changes of this kind are the mutations we hear so much about in connexion with radioactivity, and though they can be induced artificially, they occur also in nature. It is here that controversy rages. At this date there is no longer controversy as to evolution itself, as to its having been responsible for the diversity of living creatures. There remains fundamental disagreement as to the means by which it has been brought about, and it is here more clearly than perhaps anywhere else that we find the conflict between those who believe in an unplanned as opposed to a planned, purposeful and directed world. Orthodox evolutionary theory holds firmly to the first of these beliefs, maintaining stoutly that these heritable gene-mutations show no evidence of being in any way directed, that they arise spontaneously (whatever that may mean), and are governed in their appearance by the laws (if they can be called laws) of chance. This attitude arises chiefly from ignorance as to what causes mutations. When spontaneity and chance are invoked as first causes ignorance can be surely inferred. Not that evidence is wholly lacking. Study of the innumerable lines of development that evolution has taken shows signs of their having been directed by a principle of hit or miss, trial and error, some lines ending fairly soon in extinction, others persisting over long periods with scarcely any change, others again showing continuous change with steady improvement.

Believers in a planned world remain unconvinced, regarding this as evidence of the infinite variety of nature, and of ignorance as to the means of direction. They too have their evidence, do not rely wholly on conviction. They point to the fact that in the first place natural mutations in a given individual are extremely rare, in the second that the vast majority are harmful and therefore doomed to swift elimination. Above all, critics of orthodox evolutionary theory take their stand on what seems to them the total inadequacy of known mutations to produce pronounced changes, major innovations, even cumulatively over a long period of time. Individual mutations have been known to produce changes, but they are trivial changes of colour or dimension, such as might account in time for differences between closely allied species; but far more than this is required of them. They are required to account for the difference between an eagle and a humming-bird, between a bird as a bird and a reptile as a reptile, ultimately between an amoeba and the reasoning scientist who peers at it through his microscope. In addition to this, but essentially a part of it, there is the development of so complex and exquisite an organ as the eye of a mammal from the primitive eye-spot of a protozoan to be taken into account, not to mention, as we must mention, that of a speculating brain from some rudimentary nerve-centre. How can such incalculable changes have come about unless mutations are in some way directed? Chance can no more be given the status of a first cause here than elsewhere, though it is true that those who reject chance are unable to offer any clearly defined alternative. They prefer to plead ignorance and await enlightenment.

Natural selection on the other hand, acting on hereditary variations, in whatever way these have been brought about, weeding out the unfavourable, preserving the favourable, is not to be denied as a cause, probably the most important cause, of the adaptation of animals to their environment. Evidence in its favour is overwhelming, and its continuous operation as a great natural agency, playing its part with other agencies, offers no violence to the concept of a planned scheme. At the same time

there is good reason to suppose that other factors have been and are at work. There is no need to give it exclusive dominion over the lives and the development of living creatures. Some of these other factors are dealt with at the end of this chapter. There is wisdom, therefore, as well as humility, in admitting that our understanding of mutations, the raw material of evolution, is extremely limited to say the least. As for the result of the interaction of the two down the ages, it is there before our eyes in the form of the diversity of living creatures, and we are entitled to represent it as a sort of family tree, beginning with the protozoa or perhaps with the bacteria and the viruses and ending with man. But a tree is a somewhat misleading figure of speech, since it suggests a single main stem with branches at the sides. A more accurate figure is some kind of shrub, with a number of leading stems united near the ground, each one dividing and sub-dividing a great many times.

Three phases of operation

Looking upon the whole process from this point of view, we can make a distinction between three phases of operation. The first is a matter of slow, continuous change in a single constantly maintained direction, the results of which have often been found in a series of fossils, such as sea-urchins in chalk, or some kind of mollusc in limestone. Such a series of fossils corresponds with, is found within, a certain thickness of rock laid down without a break, and without marked change, in some long-vanished sea. Here the rock is the fossilized environment and the fossils are the creatures that lived within it. The topmost, that is to say the latest fossils of the series, say, of a sea-urchin, may show a distinct difference in shape, or in the arrangement of the grooves of what was once the shell, from those of the lowest or earliest, while those in between are continuously intermediate. The differences may be sufficiently marked so that two distinct species, or more probably subspecies, can be made out. It is very unlikely that any greater degree of differentiation will be noticeable.

To take another example of the same process, there is a common Jurassic fossil, a mollusc known as *Gryphaea*, with a curved, that is to say a convex, shell. A series of *Gryphaea* fossils often shows a graded differentiation in curvature from the lowest to the highest. In both these examples the time represented by the change, which is the time taken for the deposit of rock to be laid down, might very well be some hundreds of thousands of years, which seems long to us, but is no more than a brief interlude in the span of geological time. In both instances too the environment would be relatively constant.

But there is an interesting and important distinction between the developments undergone by the two kinds of fossil. In the sea-urchin it was a matter of shape, or of the arrangement of grooves: in the mollusc one of curvature. In what way could a difference of shape or of pattern give advantage to the sea-urchin? We cannot say, and conclude that they give none. They are examples of characters known as non-adaptive, and there are a great many of them in the animal kingdom. With *Gryphaea* on the other hand we can see an advantage, since an increase of curvature would enable the creature to protrude more easily above the mud for feeding purposes. Curvature, therefore, may well be an adaptive character, and we can see how natural selection in all probability worked. With the sea-urchin we cannot do so. There are two possible ways out of the difficulty. A pear-shaped rather than a circular outline, or some difference in the arrangement of grooves, may give advantages we are unable to understand. That is perhaps rather too easy a way out, even if it shows signs of a becoming scientific humility. Alternatively, it is possible that either or both of these characters may be linked up genetically with others we are unaware of and which are adaptive. They might, for instance, be linked up with a greater degree of hardiness, the ability to stand up to some slight and undetectable change in the environment. It may as well be confessed here that the problem of non-adaptive characters is one that bristles with difficulties. I shall have more to say of them later.

The second phase of evolution in action involves changes of a much more marked kind. Let us glance at the evolution of birds. They evolved, of course, on dry land, a medium giving a far greater choice of habitats than the sea. Birds we know evolved from reptiles, but for the moment I will leave that sensational, though certainly not abrupt, step on one side, and focus attention on some hypothetical creature half reptile and half bird. As it happens such a half-way creature is not altogether hypothetical. I have referred already to that very remarkable fossil, *Archaeopteryx*, the priceless treasure of the British Museum. It was a winged reptile, but not in any way a winged lizard of the pterodactyl type, since its wing-structure was that of a bird and it had feathers. At the same time it had teeth and a tail, not of feathers only but of bone as well, an extension of the spinal column. These are reptilian characters. It was about the size of a crow, and almost certainly it fluttered rather weakly from branch to branch, being as yet no more than a pioneer in the art of flying. The pterodactyls had acquired the art, but it had been forgotten and had to be learned over again by the birds. Incidentally this is quite a common occurrence in evolution. Some notable skill evolves independently three or four times. The art of flying, for instance, was acquired independently on some later occasion by one of the mammals, the bat, just as it had been learned by the insects millions of years before the first reptile or the first bird existed.

Now it is most certainly true that *Archaeopteryx*, though combining in its person both the characters of reptiles and of birds, is nevertheless not to be regarded as the ancestor of all the birds that now so notably enrich the earth. What this ancestor was like we have no idea, but it may well have been more reptile than bird. All we can say is that somewhere, somewhen, and above all somehow, there arose a proto-bird, and there must have been gradual transition from the one to the other, so that it would be very difficult to point to one specific creature and decide that that one must be regarded as the ancestor of future birds. Be that as it may, what I am concerned with now

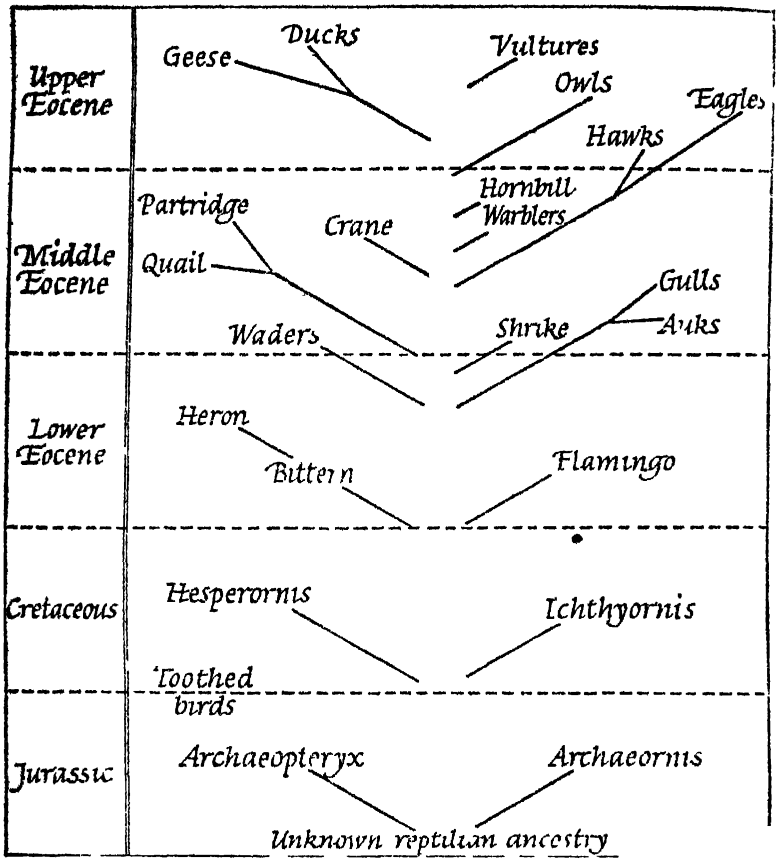

Figure 6. Diagrammatic scheme for the radiation of birds, mainly in the Eocene Period, as shown by the fossil record.

is to bring ecology into the picture, and to explain that what enormously furthered the evolution of birds was a process known as adaptive radiation. By this is meant the divergence, the fanning out, the radiation, of these proto-birds, at different stages of the process, from their original environment into a number of new ones. As for reasons for their doing so, it is possible to suggest many. It may have been because of persecu-

tion by predators, or because they happened to light upon a new, or a richer, source of food. There may even have been something approximating to choice governing their movements. That is no more than one set of reasons. Another and more probable one is bound up with change in the environment they originally knew. Environments do change, as I devoted a whole chapter to pointing out. All the while, it must be understood, heritable mutations were taking place from time to time and natural selection gave perpetuity to those among them that proved advantageous to their possessors in the new environment.

The result is this radiation into an enormous variety of birds adapted more and more closely to a variety of environments, so that there evolved forest birds, grassland birds, raptorial birds, seed-eaters, fish-eaters, water-birds, diving birds, hole-nesting birds, even birds that in time lost their wings altogether. The members of each of these, as well as of other, groups acquired characters adapted to their way of living – length of leg, stoutness or slenderness of bill, hooked bill, curved bill, webbed or lobed feet, as well as adaptations in form, size, or colour and a hundred more besides. At the same time there would appear great numbers of those characters we call non-adaptive, especially as between closely allied species, minute distinctions in colour and dimension.

All this, of course, was a slow, protracted business. Nowhere perhaps does the principle of gradualness more notably come into its own than in evolution. The process was not only slow but sub-divided, minor radiations following upon major ones. The birds, for instance, that favoured a watery environment would radiate out into different kinds of water-bird – ducks, geese, grebes, waders. Each of those groups would then split up into the various kinds of duck, goose, grebe, wader, fitting themselves as they did so into the animal communities of which they became a part, taking their places in food-chains, settling down into appropriate niches, establishing territories when the need arose, competing within the limits of competition, coopera-ting in such a way that the resources of the habitat became

portioned out between them and its other denizens, extending and complicating the great web of circumstance in which they were enmeshed.

The same thing took place with the other great groups; mammals, for instance, descended like birds from reptiles, radiating and re-radiating into herbivores, carnivores, burrowing mammals, flying mammals, swimming mammals, and all the rest. The main process is the same for every group. The same rules are obeyed. This brings me to the third phase in the working out of evolution, which in fact I could not help bringing into the previous one. It gives rise to the most marked change of all, the appearance of an entirely new type, characterized by entirely new developments. It leads inevitably to some fresh major radiation. I mean, for instance, the evolution of bird from reptile, or of mammal from reptile. Considering the second of these, we are to suppose that because of successful advantageous adaptations some reptile gradually acquired the distinguishing characters of mammals – the bringing forth of young alive rather than as eggs, the subsequent nourishment of these young by means of glands secreting milk, the acquisition of hair rather than scales, and perhaps above all the development of a thermal system giving their bodies a temperature independent of that of the world outside. It is important to remember that we really know nothing as to how such vitally important changes took place.

The effect of isolation

What has been said so far has failed to give prominence to two closely related factors having the utmost relevance to ecology and evolution. We are concerned with the animal as an intimate part of its habitat, and as a component of an animal community consisting in most cases of many different kinds of animal. There are times when a group of animals forsakes its community. That will have its place in the argument, besides being bound up with the problem of migration, to be dealt with in a separate chapter. But clearly we must begin with the conception

of the animal occupying its appointed place in the community, and for my present purpose I am concerned with the kind of animal, with the species. This is far less easy to define than might be supposed, but the essence of it is concerned with the capacity of the members habitually and successfully to interbreed. Animals of different species do not breed with one another either by habit or normally with success.

Sometimes such cross-breeding is successful in producing a hybrid, but hybrids are usually sterile. There are barriers of various kinds to interspecific breeding. Sometimes it is a matter of sheer incompatibility of size or of sexual organs. There is a physiological barrier, since the female gamete is almost invariably more easily fertilized by a male gamete of the same species than by that of a different one. Another kind of barrier is that imposed during courtship. The purpose of courtship is to arouse the sexual elements, especially the ovaries of the female, to readiness for reproduction. This is done between the sexes by means of signals or stimuli of scent, colour, sound, or posture. These are specific, each species making use of one or more innate stimulus, and the stimulus must be the right one or there will be no reply. If an animal of one species attempts to court one of another, although closely allied species, there will be incompatibility of signal and answer and the courtship will come to nothing. Finally there are barriers more strictly ecological. Members of two species in breeding condition simply do not meet because they belong to different habitats. They are spatially isolated. Alternatively they may be temporally isolated, because their breeding seasons occur at different times.

For one or more of these reasons interspecific breeding is made difficult, if not impossible. The point to be stressed here, however, is that this isolation between species, though of the greatest importance in other ways, is not the most important form of isolation where evolution is concerned. By that time, it could be said, evolution has already occurred and further evolution can only make the barriers between species yet more formidable. What is of initial, and therefore primary, importance

is some kind of isolation between members of the same species, barriers, that is to say, which will prevent or restrict intra-specific breeding. That probably sounds like a highly paradoxical statement. How can evolution be furthered by barriers against breeding? The fact that it is, and how these barriers are set up, must now be explained.

This form of isolation arises from the way in which members of the same species are distributed within the community, over the range of the habitat that is theirs, and I am thinking now of habitats in the wide rather than the narrower sense. Distribution is not haphazard and seldom continuous: animals of the same species associate in groups or populations, varying in size and complexity from a mated pair together with their offspring, to a nest of ants or a breeding colony of gannets. In between those extremes there are populations of all sizes, associated either permanently or from time to time. Other examples are a tribe of baboons, a herd of deer, or a shoal of herring. A nesting colony is very highly organized, a shoal of herring scarcely at all. These groups in fact are exactly the same as those described in some detail in Chapter 5, when cooperation between individual members was under discussion, and arise from the fact that all animals exhibit some degree of social appetite, either at all times or for special reasons such as collective security, feeding, and breeding.

This differentiation into groups, resulting in a discontinuous distribution, has a highly important cause other than social appetite however loosely manifested, and is a purely ecological concern. The two causes reinforce one another. This second cause arises from the fact that a species is required to live in a habitat that suits it, and this will be not merely a possible habitat, but the best possible. A rare species of animal, for instance, is not found widely scattered in its rarity, but in a few isolated populations wherever some rare combination of factors, or even a single factor such as the food-plant of the larva of an insect, provides the necessary conditions. Since, as we have abundantly seen, habitats are essentially discontinuous, so correspondingly is the distribution of animals.

A technical term is needed for these groups, and the word deme has been suggested. It is a good, simple term and should be widely used, not because it is a particularly attractive word, but because it has the great merit of putting an end to confusion. Aggregation, group, population, community, these are words of more than one connotation and therefore almost certain to lead to confusion and ambiguity. A deme is a deme and nothing else. All species then are to a varying extent broken up into demes, and the things that the members of a deme have in common are the capacity to associate in some sort of communal existence, and the capacity to breed among themselves normally and successfully.

This breaking up into demes is of such importance that it is not too much to say that without it evolution would never have taken place. The result of the breaking up is that there must exist some degree of isolation between one deme and the next, isolation that in most cases restricts and in some totally prevents interbreeding between members of two different demes. Why should this form of isolation be so important? Because otherwise any advantageous mutation, calculated to lead to a change in the evolutionary history of the species, would almost certainly be swamped by interbreeding before it had a chance to establish itself. Given only a partial isolation, there will be a reasonable chance of its spreading so that natural selection can get to work in its favour.

The point must now be enlarged upon so as to make more clear the causation of demes in the first place and the way isolation can be made more pronounced. Perhaps enough has been said as to their initial causation, but nothing in nature stands still, and there is a whole host of ways in which isolation between demes can be brought about and intensified. In the first place there is bound to be correlation between the size of demes and the degree of isolation. The African savanna is a habitat of great extent, and a deme of some highly mobile and socially inclined creature such as the zebra will be correspondingly large. Isolation will not readily occur, but even so is bound to exist here and there, one deme separated from another

perhaps by a wide strip of country too arid to provide them with the grazing they require, or by the gorge of a river with precipitous sides. The deeps of the ocean constitute an even larger habitat, and oceanic demes can hardly fail to be correspondingly immense. At the opposite extreme, the smallest of demes will be the most completely isolated, and will diminish in size all the way down to short-lived salt-pans in the African savanna, or water-filled hollows in decaying trees, inhabited by rotifers and the larvae of midges.

The problem arises as to whether the influence of environment can be said to conform to any recognizable laws, and there is no doubt that with widely-ranging species, particularly perhaps birds, that it does. There are in fact a number of such laws. One is that with a population of the same species stretching over several degrees of latitude, those members inhabiting polar regions have a distinct tendency to be larger than those living nearer the equator. Another states that in that part of a range of a species having a relatively low temperature, appendages such as bills, tails, ears, are shorter in proportion to the body than when the temperature is higher. A third establishes a correlation between warm, moist conditions and a dark coloration, between warm, dry conditions and tints of yellow. Yet another, applying to birds, is that those living in cool regions tend to lay more eggs than members of the same species living where it is warmer. This is interesting since the governing factor seems to be length of day rather than temperature, and it means that birds nesting in cool, high latitudes can feed more nestlings because there the summer day is so much longer than the night.

One very important result of these environmental changes is that the animals at one end of a range of distribution extending over several degrees of latitude may differ quite considerably in size, colour, or markings, from those at the other end. Sometimes the variation in a character can be traced continuously and smoothly from one end to the other: more often it is discontinuous, as it were, in steps. Such widely-extended spatial variations of both kinds are known as clines, and it is supposed

on good evidence that they are important in evolution, since a smooth cline is likely to develop into a stepped cline, thus dividing the species into demes, each one isolated in some degree from its neighbours.

Looked at thus dynamically, considering, that is to say, both the setting up of isolation and its intensification, the possibilities are seen to be almost endless. Isolation may arise through the action of the animals themselves in removing themselves, perhaps because of intense persecution by predators, or in order to exploit some new source of food, from one habitat to another. Either of these could result in the splitting up of a deme into two or more. Another set of causes, almost certainly commoner and more influential, arises from the diversity of the earth's surface, and particularly because that diversity is continuously and slowly changing. These causes in fact are essentially geographical and may well be exerted over wide areas. Among them are outbursts of volcanic activity, the slow heaving up of mountain ranges, invasions and withdrawals of the sea, the work of rivers, glaciers, the wind, changes of climate, and all the great, secular heavings and warpings of the earth's crust, a few sudden and violent, most rhythmical and recurring, all from our point of view exceedingly slow. Clearly their influence in the splitting up of populations into demes has been varied and immense, beginning at the time when life first came into existence, as important today and in the future as ever they were throughout the long history of life on this planet. The isolation they brought about between demes has frequently been complete.

In any such deme of a species, isolated from other members of the same species by some geographical or climatic barrier, it is possible that an advantageous mutation may arise, which natural selection may favour and perpetuate. But even if no such mutation occurs the effect of isolation is still of the utmost importance since it will mean that over a long stretch of time, during which the deme is becoming more and more closely adapted to its environment, each member will acquire an equipment of hereditary factors nicely adjusted to local conditions.

Between members of the deme a constant exchange of these equipments takes place, and the result is a harmonious, collective genetical constitution. Because no two environments are exactly alike it follows that no two genetical constitutions will resemble one another in every respect. They will differ slightly or considerably: certainly to some extent, and this means that the raw materials of a new species have appeared. For fulfilment of the process we need not continued isolation but its opposite, the breaking down of barriers, so that members of two isolated demes can come together. It is not until then that the rise of a new species can, so to speak, be proclaimed and made absolute. Such a meeting of previously isolated demes may take place actively, because of the migration of some or all its members, as frequently happens with birds. On the other hand, if the species in question be of some less mobile creature, then the meeting is more likely to be passive, brought about by the gradual, or possibly fairly sudden, disappearance of the barrier which hitherto has kept them apart. If in the course of the earth's long history barriers of one kind or another are frequently set up, so with corresponding frequency may they be lowered.

Now, what happens when two previously isolated demes of the same species come in contact? What is the test by which we judge whether or not a new species is on the way? There can be one only: whether or not they interbreed with success. If the divergence between them is no more than slight then in all probability they will merge and no new species appears. That is one extreme. The other is that the two demes have so widely diverged that no successful interbreeding is possible, which can only mean that a fresh species is born. But clearly we must take account of intermediate conditions as well. Members of two meeting demes may mate, giving rise to a hybrid which is the result of the mingling of two divergent, but not widely divergent, genetical constitutions. When that happens there is certain to be some degree of discordance, with the result that the hybrid finds itself at a disadvantage in the battle of life, as compared with its parents. This has been proved with respect

to members of the same species of frog (*Rana pipiens*) from widely separated parts of the United States. The more widely separated they were, in this instance by barriers of climate, the more pronounced was the tendency for hybrid embryos to die at an early stage of their development.

The agency at work is, of course, natural selection, which in this way works so as to encourage breeding between members of the same deme and to discourage it between members of different ones. The offspring of the first is likely to thrive, that of the second to disappear. Thus, although the physical barrier which once separated the two groups no longer exists, its place is taken by a barrier of quite another kind, one which prevents or at least hinders breeding between members of divergent demes. The divergence is accordingly fostered and enhanced, which means that outward and visible divergencies, arising from the general, inward, genetical divergence are certain to be favoured by natural selection, and not favoured merely but intensified. Incompatibilities of one kind or another will then be at a premium. Examples have already been given (see page 171) and this is where they become important. Any incipient tendency to breed at different times of the year will become something more. A slight incompatibility in the size or structure of sexual organs will tend to become complete. Signals of behaviour or coloration exchanged during courtship, if initially slightly divergent, will become more so, until they fail to give rise to the appropriate counter-signal, with the result that no mating takes place. In any one or more of these and other ways the divergence between the two groups becomes wider, until in time there can be no mistaking the fact that where formerly there was one species there are now two.

Here then is one, and almost certainly an important and frequently occurring, method by which evolution operates. It could at least account for the features distinguishing closely related species. Very possibly it could go a good deal further. One or two examples will help to make this clear. Over the mainland of Scotland and the islands of the western and northern coasts there are found four subspecies of wren. One is

confined to the mainland, a second to the Shetland Islands, a third to the Outer Hebrides, a fourth to the far island of St Kilda. These four differ slightly in size and colour, rather more so in length of wing, and the differences seem to us to be non-adaptive. Very probably they are when considered separately, though they may well be genetically linked to others that are adaptively significant. Distinctions between subspecies on the one hand, and closely allied species on the other, are very frequently of this kind. The variations in wing-length are slight enough, a matter of a few millimetres, the wings of the St Kilda wren being longer than those of the mainland form by some ten millimetres. Each of these wrens is thought of as a separate subspecies, and it seems reasonable to regard each as a species in the making. They are differentiated demes of the species wren, prevented from interbreeding, as presumably they would be capable of doing, by their isolation from one another, that complete, primary, geographical isolation caused by the slow drowning of the coastline, probably since the end of the Ice Age, which has transformed mountains and mountain ranges into islands.

Parallel examples come from much more distant parts of the world. In the Society Islands there are various species and subspecies of snail found in wooded valleys separated by high mountain ridges. Here it seems probable that in some instances isolation has broken down, or been overcome in some way, so that new species have arisen in comparatively recent times. It is very significant that some of the differences between these valley-dwelling snails were found to have become intensified when re-examined after as short a time as fourteen years. Another example comes from the great island of New Guinea, where demes of a species of cockatoo have established themselves, distinguishable again by length of wing. The cause of differentiation here is obscure.

By far the most interesting example comes from the Galapagos Islands, some 600 miles off the coast of Ecuador. Distributed over these islands, and unknown on the mainland or anywhere else, are several species of finch, related to one an-

other, but now easily distinguishable into warbler-like finches, cactus-eating finches, ground-finches, tree-finches, and finches that resemble woodpeckers. The important point is that what now separates one species from another is not a stretch of sea between islands, but a way of living, a feeding-habit, an ecological niche. Two or more of these kinds of finch may be found within the same broad habitat on one or another of the islands, but the fact that one feeds on large seeds, another on smaller seeds, a third on insects, means that they do not compete, are ecologically isolated. It is significant that these differing habits are reflected in differing sizes and shapes of beak. How did this highly interesting state of affairs come about? Clearly we can never know for certain, but it seems there can be little doubt that it began when at some time in the remote past a single, undifferentiated finch-stock invaded the islands, split up from island to island, and settled down. A number of these isolated island populations or demes began and continued to diverge from one another. Then for some reason one of them invaded a neighbouring island, came in contact with a related finch population, but because the two had diverged failed to hybridize with it. A new species of finch was born. This same process could well have been repeated many times until as now the original finch-stock split up even beyond the limit of species, and can be divided by systematists, not merely into distinct species to the number of fourteen, but these fourteen into four separate genera.

One more point is worth making. These finches aroused the interest of no less an observer than Charles Darwin, who was deeply impressed by them, when in 1835 the *Beagle* visited the Galapagos Islands. Dr David Lack, who studied them at a much later date, calls them Darwin's finches, and it is a pleasing thought that these birds played a part of some note in Darwin's prolonged meditations which in 1859 found fruit in *The Origin of Species*.

The influence of density

The density of a species of animal over a given area of the habitat was referred to in Chapter 4, and it was pointed out then that with many, notably the fur-bearers of the Canadian tundra, this density fluctuates within very wide limits and with a strange regularity. These fluctuations and particularly their cyclic regularity are far from being clearly understood, but there is no doubt that they are important in evolution. This is to be found in the way in which natural selection acts with an intensity varying according to the different phases of each complete cycle. There are four of these phases succeeding one another always in the same order. First there is a phase of decrease, a thinning of numbers, when natural selection is bound to be active and powerful. It is in fact the high death-rate produced by selection that causes the decrease. Next comes a phase of minimum density, when the animals are markedly scarce. At this time natural selection continues to be severe. More than this, adaptation will be important at such a time, since only those individuals closely adapted to their environment are likely to survive. For this reason any advantageous mutation that may be present is certain to show itself in a higher proportion of the population than earlier. Consequently adaptive evolution will be speeded up. Arising from this is the important principle that an exacting and perhaps changing environment is likely to give rise to closer adaptation than a favourable and relatively constant one.

Phase three is one of steady increase when selection will be weaker, since at such a time many individuals that would perish during a decrease are then managing to survive. This means that an increasing population is more variable than one that is standing still, and that adaptation is less likely to take place. As soon as the fourth phase, one of maximum density, of intense pressure of numbers, is reached, selection again becomes active; and adaptive variations, correspondingly important, are likely to establish themselves once and for all.

An interesting and rather difficult problem is that connected with variations that are non-adaptive, those so far as we can see, that give no advantage to their possessors. If these are disadvantageous they are almost certain to be eliminated, at least at those times when selection is actively at work. On the other hand it seems reasonable to suppose that a great many of them will be neither the one nor the other, as we might say neutral, and it has been suggested that during phases of increase these are likely to spread with some rapidity, unaffected by selection. This might explain their notable frequency, serving as so often to distinguish subspecies, such as the Scottish wrens, or closely allied species from one another.

Evolution in action

I hope it is now clear that the relationship between ecology and evolution is an extremely close one, and in particular that a changing habitat is extremely likely to play a major part in furthering organic change among animals, giving renewed scope for natural selection to perpetuate advantageous hereditary mutations, however brought about. Considered against the background of the long history of the earth, it can be said that habitats scarcely cease changing.

The examples already given, of which the purpose was mainly to stress the importance of isolation, are of the greatest interest, but are concerned with relatively unimportant changes. The Scottish wrens, the Galapagos finches, the New Guinea cockatoos, provide evidence of differentiation in respect of minor characters of wing-length and colour, such as may account for differences between subspecies, species, or at the most genera. Significant though they are, they can hardly satisfy us as examples of evolution in action, since what we naturally demand to be shown are examples of changes of a far more marked kind. These further, more impressive examples, major events, that is to say, in the history of life, I now propose to give.

The first example is impressive, not because the change could

conceivably be described as a major event, but because it shows that the process is still at work among us, and that noticeable change can come about in a surprisingly short space of time. The actors are certain moths, in particular the peppered moth (*Biston betularia*), though another, the scalloped hazel (*Gonodontis bidentata*), deserves mention as well. About a hundred years ago, during the earlier half of the nineteenth century, both these moths were known over this country in what must be called their normal pale-coloured form. Since about 1850, however, there has appeared a black variety in steadily increasing proportion and confined mostly to the industrial regions of the north. Today the black variety is the rule in Lancashire and Yorkshire, while moths having the pale coloration are exceptional. In the rest of the country conditions are the other way about. The conclusion is clear, has been confirmed by experiments and provides us with an admirable example of the effect of natural selection. The air in industrial districts is polluted by particles of soot laying a black film, as some of us know only too well, on leaves, tree-trunks, and fences. Here then was a change in the habitat brought about rapidly by human action, and it has resulted in a correspondingly rapid change in the coloration of these moths. For it was not soot-particles that caused the changed coloration of the moths, but a black pigment known as melanin. The process is referred to as industrial melanism and is caused by a mutation, the work of a gene or combination of genes causing blackness. The point is, of course, that in the now industrialized habitat to be black is an advantage, an example of protective resemblance. Selection acts in favour of the black mutation and against the normal pale colour. In the southern part of the country black varieties are occasionally found, but natural selection sees to it that they remain comparatively rare. This means that the gene, or combination of genes, causing blackness was present in the hereditary complex of the moths before the Industrial Revolution, and that it was only when man brought a blackened habitat into existence that selection could act in its favour. As an example of the way in which genes have a multiple effect, it can be added

that the mutation we are concerned with causes not blackness or melanism only, but increased hardiness in the larvae as well. There was thus an additional reason for the establishment of melanism.

It is a far cry from moths to extinct reptiles, and there is a notable contrast between the second example and the first in another respect, since we are concerned now with what is unquestionably a major event in evolution. Consider the dinosaurs, that group of reptiles which lorded over other forms of life for the greater part of the Mesozoic or middle era of evolutionary history, ending some seventy million years ago when they vanished for ever from the earth. In spite of this wholesale extinction, they have as a group little cause for complaint, since their day of dominion endured for part of the Triassic, the whole of the Jurassic and the whole of the Cretaceous Period, amounting in all to something like a hundred million years. There were, of course, other reptiles, notably the flying pterosaurs, and the dinosaurs were of two orders distinguishable by the structure of the pelvis. We are much inclined to think of them as enormous and it is true that some of them were the largest land animals that have ever existed. Others were not much bigger than hens and there were many of intermediate size. They provide us with yet another example of adaptive radiation, perhaps the strangest that ever took place. What caused their extinction?

The popular notion, obsessed by the thought of huge dimensions, inclines vaguely to the conclusion that they grossly overplayed their roles, became too enormous for their strength, failed to develop a brain in any way proportionate to their size, went in for grotesque horns, crests, and armour-plating, that in short it was their very evolutionary exuberance that laid them low. There is a modicum of truth in this, but it is a wrong approach to the problem. Far better to take an ecological view. With regard to the giants it is true that some were so prodigiously large that they found it necessary to spend most of their time in water, wading in immense swamps, browsing almost incessantly on rank, aquatic vegetation. They needed the

support of the water to buoy them up. But life must have been easy enough, apart from the menace of the carnivorous dinosaurs that preyed upon them, so long as their habitat remained unchanged. We have good reason for supposing that the habitat of most of the dinosaurs did change, in particular the immense swamps together with the hot, humid climate responsible for them. At the end of the Cretaceous Period and at the beginning of the Tertiary Era that followed, there began a great phase of mountain-building, heaving up what are still the great ranges of the world, the Himalayas, the Alps, the Rockies, and the Andes. Continental interiors were slowly rising, climatic conditions became colder and drier. This meant that swamps could no longer exist, that the plants that were the food of the great herbivorous dinosaurs like *Diplodocus* and *Brontosaurus*, as well as of the smaller forms, gradually disappeared. With them disappeared of necessity the carnivorous dinosaurs as well. It was in this way, in all probability, that the Age of Reptiles came to an end.

Pre-adaptation

Two more examples of major events in evolution remain to be described, both concerned with positive achievements, of which one is not so much important as momentous. In dealing with them I shall refer at some length to a factor in evolution which has not yet been mentioned, not because it played no part in events already described, but because in these two we find unmistakable evidence for the part that it played in materially assisting the structural response of an animal to a changing environment. It is for this reason that I deal with these examples under a fresh heading

What are the two most striking general results of evolution? First the animals undergo organic change, one type evolving into another type. Equally important for my present purpose is the other: that all kinds of animal existing at any one time are adapted each to a certain environment. The degree of adaptation varies, as we have seen, within wide limits, all the way from

a loose, so to speak elastic adaptation permitting more than one environment to be suitable, to extreme specialization with regard to one kind only, frequently of a very restricted sort. The all-important point is that adaptation must exist or the animal will be unable to maintain itself. From this it follows that when an environment changes, its tenants, having already adapted themselves to one set of conditions, must contrive to adapt themselves to another set. If, like the dinosaurs at the end of the Cretaceous Period, they fail to do so they will inevitably perish. They must be capable of surviving the change, of setting up at least a bridgehead of survival in the new environment. Now it is, of course, true that the ability to do this up to a point is inherent in all animals. They are quite capable of changing their habits, of living, for instance, on some new kind of food. This means that when changes are slight, as most of them are, the problem of survival presents no great difficulty. But where major changes are concerned, such as that from forest to grassland, something more will be needed if the animal is to have a reasonable chance of surviving.

Changes of both these kinds, the slight as well as the more marked, necessitate differing degrees of what is known as pre-adaptation. To consider slight changes first: when an animal transfers its attention from one foodstuff to another its digestive system must be of the kind that is in the first place adapted to the original food and at the same time in a sense pre-adapted to the new one. Very possibly it will be suitable for both, and the transition is then easy. That is an example of one kind of pre-adaptation, inherent and universal in a wide variety of ways. But there is also another and more specialized kind, when an organ or a limb that has become adapted to a certain set of conditions, and used for a particular purpose, is capable of becoming modified for use for another purpose in a different set of conditions. For this to happen it is essential that the organ or the limb should possess already some feature capable of adapting itself to changed conditions. It is as though (and why not?) the change had been foreseen and allowed for in the course of the animal's evolution.

We can now come to specific examples of evolution in action and the important part that this more striking kind of pre-adaptation played in it. First, consider the development of the modern horse. This is a story that has been told many times. Almost every book on evolution brings it in, often in considerable detail, which is not surprising for it is one of the very few tolerably complete sequences that the fragmentary fossil record can show. Once more ecology plays a major part. The evolution of the horse must have involved organic changes of many kinds, but naturally we can know only those that show themselves in the fossilized skeleton, and of these, four are outstanding. They are: an increase in size, a reduction of the number of toes or digits on all four feet, an elongation of the facial region, and finally a marked change in the teeth. The earliest horse, *Eohippus*, was about the size of a fox-terrier, had four digits on each foot, and low-crowned teeth adapted to browsing off comparatively succulent vegetation. Subsequent development, culminating in the horse we know and protracted over some fifty million years, was towards a progressively larger animal with a more highly developed brain. Accompanying these changes there arose a tendency towards supporting the weight more and more on the tips of the toes, in such a way as to make the lateral digits less and less necessary. This gave the creature enhanced speed, and it ended in the single-toed horse of today with vestigial splint-bones, invisible externally, as the sole remnants of the lateral digits. As for the teeth, they underwent a change from the low-crowned sort with a simple surface-pattern, to a new type longer in proportion to their width and with an intricate surface-pattern suitable for the mastication of harder and drier grasses. All these changes were adaptive, for the later horses were grazing as opposed to browsing creatures, and their development can be correlated with a changing habitat during the Miocene Period when forests were tending to disappear and drier, open, grassy plains, admirable for galloping over, were taking their place. Life on these plains set a premium on speed and on the ability to chew tough-stemmed grasses. But it must not be supposed that there was this one line

of development only. On the contrary there were many lines, but none persisted for as long as that which gave rise to the large, one-toed, grazing horses. One line continued from the original forest-living browsers, which remained as such. They too developed, but differently and less rapidly, reaching a sort of culmination, with three toes instead of four, at about the time when the future grazers were beginning to take to the plains. Finally they became extinct.

How then does pre-adaptation figure in this story? Very notably. One example of it has already been referred to, namely that the forest-dwelling browsers, while they could still be so described, had undergone a reduction in the number of their digits from four to three. But that is by no means all, for the interesting and highly significant conclusion emerging from study of the skeletons of the many kinds of horse destined in time to develop into the animal that we know today, is that their evolution was materially assisted by organic changes that had already begun to manifest themselves while yet they lived in forests and browsed off leaves. In other words those structural changes fitting them so admirably for life on the plains began to develop before the conditions responsible for their final perfection had begun to appear. The browsing forest-dwellers in a word were pre-adapted in a number of ways for life on open plains, where under stress of natural selection these same characters were yet further modified, adapting their owners more and more closely to the new way of living. The same may well have been true for other characters, a digestive system, for instance, adapted in the first place to the use of comparatively soft plant-food, and perhaps in some way pre-adapted for dealing with tough grasses. Since there is no possibility of stomach and intestines being handed down to us in a fossilized state, this can be no more than conjecture.

Another and perhaps even more striking example of pre-adaptation involves a more pronounced change of environment and an incomparably more important step in the evolution of life. It concerns the evolution of amphibians – frogs, toads, newts, and the like – from fishes, of creatures, that is to say, in

their adult stage habitually breathing air by means of lungs, from those at all times breathing oxygen dissolved in water, by means of gills. It is generally agreed, both on biological and geological evidence, that this momentous step, without which the evolution not of amphibians only, but of reptiles, birds, mammals, and ultimately of man himself, could scarcely have occurred, took place some time in the Devonian Period more than 300 million years ago. The environment concerned was that of shallow, fresh-water lagoons under a hot, moist climate. Lagoons of this kind are well known today, wide stretches of shallow water, overshadowed by luxuriant vegetation, intensely heated by the sun, subject to a high degree of bacterial decay, where photosynthesis is at a discount and conditions generally those of stagnancy and a low content of oxygen. Life is not easy in these circumstances and the fishes exploiting them must adapt themselves or perish. What is particularly required of them is to perfect devices enabling them to make the most of the small amount of oxygen available, and this many of them have achieved by means of what may be called proto-lungs in their gill-chambers, air-bladders, stomachs or intestines. Because of these they can take in air from above the surface of the water. Nor is this all, for it is known that fishes living in stagnant, tropical waters have evolved a type of blood which differs from the blood of other fishes. The difference is to be found in a lack of sensitiveness to carbon-dioxide. Stagnant waters, while poor in oxygen, are comparatively rich in carbon-dioxide, and this richness in carbon-dioxide makes it difficult for the blood to transport oxygen; so a type of blood insensitive to carbon-dioxide is essential for fishes living in stagnant waters, where oxygen-content is in any case low. This type of blood then is an essential prerequisite for the evolution of a proto-lung.

Now, as I have said, it is reasonably certain that the fishes of the Devonian Period that evolved into air-breathing amphibians did so in conditions similar to those governing the fishes we know today that have remained faithful to the exacting environment of stagnant tropical lagoons. They were pre-adapted to an utterly different environment in these two highly important

respects, possessed blood of a kind that made it possible for them to evolve a proto-lung, and, having acquired a proto-lung, were then in possession of an organ capable of being modified into a fully functioning lung when, because perhaps of the drying up of their shallow lagoons, they were faced with the necessity of making the first tentative attempts at living on dry land.

Surely it is quite impossible to deny that this pre-adaptation, on the one hand among the ancestors of the modern horse, on the other among those of amphibians, is a factor of the utmost significance in evolution, not only when we try to explain how it operated, but also and more important when we try to make out what lies behind it. Other examples are known, and there must be others again that are at present unknown. How have they come about? Why were they at hand so as to be capable of further and different development when the need arose? The orthodox school would have us believe that the sole explanation is chance. The great god Chance once more! These pre-adapted characteristics, they insist, proved useful and important in a changing environment because they happened to be there already, achieved a limited degree of usefulness and importance before the environment began to change. It is enough to say that those of us who refuse to apotheosize chance prefer to see in it striking evidence in favour of some directing intelligence.

There is more to be said on this subject of design in the universe, incomparably more. A far larger amplitude can be claimed for it than I have attempted to show up to now, and the fact that further evidence comes not from some rebellious amateur, but from a professional zoologist makes it all the more significant. In Penguin's *New Biology*, No. 22, 1957, there appeared an article by L. E. R. Picken which opens up the most exciting possibilities, a new window on the world no less. The subject of the article is the stinging capsules, or nematocysts, with which many sea-anemones, jelly-fish, and the common fresh-water hydra, paralyse or kill their prey. These stinging capsules, each enclosed in a cell, take the form of a minute bag within which lies a coiled tubular thread in a state of tension.

When an external trigger-like bristle sets off the device, the thread is shot out of the capsule at a speed too great for the human eye to follow. As it shoots it turns itself inside-out so as to expose a surface closely set with barbs. But it does more than turn itself inside-out: it also swells in a highly specialized way, unequally, more in one direction than another. This is clear from the change undergone by the pattern of the barbs as between the discharged and the undischarged condition.

The author of the article is concerned with the mechanism of this kind of stinging capsule so far as it is known, which is not very far; but he is concerned even more with its evolution, and it is there that he penetrates that cloudy region in which biology touches closely upon molecular physics. The chain of reasoning involves abstruse technicalities and is not always easy to follow, but as I understand it there is substantial reason for concluding that this device of unequal swelling of the discharging thread has been prepared for far in advance, not merely by the structure of the cell concerned, but by the pattern of the laying down, the orientation, of the molecules at about the lowest level at which living matter begins to be built up. The conclusion arrived at is that we are faced with two conceivable alternatives: either that this planning far in advance to allow for a future contingency is imposed from outside by some directing intelligence, or that it is something inherent in all living matter. The plain man might be excused for finding the second alternative difficult to grasp, and for concluding that the two of them amount to the same in the end, namely a directing intelligence. Dr Picken finds both of them disturbing, the second rather more so than the first. Disturbing or not, it seems reasonable to regard the whole conception as pre-adaptation of the most far-reaching kind, applicable not only to the stinging capsules of coelenterates, but to living structures of all kinds, and if of living matter then of non-living matter as well, from the infinitely small constituents of the atom at one end of the scale, to the infinitely enormous swirling nebulae of outer space at the other.

More controversy

Evolution is still a highly controversial subject, and it is quite idle to pretend that we have anything like a complete knowledge of it. It will be fitting to conclude this chapter by stressing the deficiency in our knowledge and referring briefly to one or two further considerations, from which the principal point emerging is that perhaps we are wrong in assigning so dominant a rôle to natural selection, extremely important though it almost certainly is. It may even be that not all important changes are to be attributed in the first place to variations in the hereditary complex of genes. To take natural selection first, it is clear that it can favour only those variations that are adaptive, that confer an advantage of some kind. There must have been many of these, but there were also a great many that, as far as we can see, could not have been in any way adaptive. Very frequently, as I have already pointed out, they are trivial, minute features of no conceivable advantage, slight differences, say, in the colour of hairs on the tail of a mouse, or of the feathers of a bird. Now the significant thing about these trivial, so to speak neutral, characters is that the features distinguishing closely allied species, and still more subspecies, from one another are very frequently of this kind. How then have they become established if natural selection is the only external factor at work?

Part of a possible answer was referred to under the heading of density, and especially with respect to those cyclic fluctuations to which many animals are subject. It was pointed out there that during the phase of increase in density natural selection operates weakly, from which it seems to follow that this phase would also be that when non-adaptive, trivial characters get their opportunity to spread. If such characters, besides bringing no advantage, brought no disadvantage either, some at least would stand a chance of becoming established.

Another factor deserves consideration. It is well known that not by any means all the habitual acts of an animal are innate or

instinctive. Many are acquired or learned, particularly in the case of young animals imitating their elders. It is now known, for instance, that while the song of many birds is innate, that of others is learned by imitation. Chaffinches have recently been grouped in distribution from one part of the country to another in song-dialects, so that it is possible to distinguish the song of a chaffinch living in Yorkshire from that of another found, say, in Sussex. Now this, of course, is imitation, but it deserves to be called something more. It amounts to the setting up of a song tradition, or not to stretch the point too far, of education.

Let me give another example, this time from personal experience. I once saw two thrushes on the gravel path of my garden. One was an adult, the other a rather more than half-grown fledgeling, an adolescent in fact. The adult had a snail in her bill. She struck it once on the path, then instead of repeating the action, as thrushes normally do, she waited, so to speak, pointing at the snail in a half crouching attitude, with head and bill stretched out towards it. Meanwhile her offspring also regarded it, though less intently. That, most regrettably, was the end. Someone came along the path and both birds flew away, leaving the snail behind. I have never seen the same thing since, but am satisfied that what I saw then was the elder thrush teaching the young one how to deal with a snail. If that is not education, the passing on of an acquired skill from one generation to the next, what can it be? The point, of course, needs to be proved by experiment, so as to find out if in fact hand-reared thrushes, that have had no chance of learning from their parents, do or do not know how to crack a snail. If they do not, it would follow that the knack is an acquired one, and my observation would be evidence, however fragmentary, that it is part of the educational system prevailing among thrushes. The interesting conclusion would follow that this has nothing to do with heredity, that habits can be passed on from parents to offspring by education, as among men. The further point can be made that while this is not a matter of mutation, has no connexion with the gene-complex, natural selection does enter

into it, since it is logical to suppose that thrushes well tutored in the art of snail-cracking are better equipped than those untutored. Is it fanciful to conclude that education plays a part of some importance in the evolution of animals?

9

INSTINCT AND LEARNING

Reasoning at every step he treads
Man yet mistakes his way,
Whilst meaner things, whom instinct leads
Are rarely known to stray.

WILLIAM COWPER: *The Doves*

REFERENCE at the end of the last chapter to the art of snail-cracking among thrushes, and the possibility that this art is passed on from generation to generation by education, leads directly to the problem of animal behaviour as a whole, to the study and analysis of the things that animals do in their daily lives, and of what makes them do these things. This is a science in itself and one that has made notable strides during the last thirty years. So much attention is now being given to it, so many specialists devote all their time to this one branch of biology, that its inclusion in a book on ecology might be questioned. There are in this country an Association for the Study of Animal Behaviour, and on the other hand a British Ecological Society. The two are quite distinct. In spite of this there is no difficulty in justifying the inclusion. After all what is animal behaviour but a specialized and highly important part of the animal's response to its environment, and what is that but ecology?

We are concerned with the behaviour of animals from the point of view of the psychologist, and must distinguish all the way through between two kinds of behaviour: that which is innate, inherited, or as we so often say instinctive, on the one hand; and that which is the result of learning and is not inherited, on the other. This is a much less simple distinction than it sounds, and in fact it is never easy to say in any particular case whether an action is prompted by instinct or by learning. Very frequently it is a combination of the two, the latter extend-

ing the scope of the former. A young bird, for instance, in pecking for food obeys instinct, but also has to learn to distinguish between what is edible and what is not. That is only one example; others are easy to find. Apart from such major considerations learning becomes important when conditions change, or are slightly abnormal.

Instinctive actions vary very widely in complexity. On the one hand there are short, simple acts like finding and feeding on suitable food, or mating with a member of the opposite sex (Plate 6a). On the other hand there are complicated, protracted, and continuous actions like the spinning of her web by a spider, or the building of her nest by a bird. Instinct is closely linked with courtship, with rivalry between males of the same species, with care for the young, with the onslaught of predators on their prey, as well as the escape or protection of prey from predators. Examples of acts involving learning are less easily singled out, at least as far as animals in their natural surroundings are concerned, and this for the reason already given that in many cases the occasion for them occurs abnormally. It is not surprising, therefore, that investigation into the learning ability of animals has been carried out for the most part in laboratories, where tests are imposed and the results noted, as for instance the time taken by rats to find their way through a maze. Instinct then is best studied in the field, learning in most cases in the laboratory. This is something of a weakness, and clearly it would be better as far as possible to carry out learning tests also in the field, so as to make them conform to natural conditions. In the daily life of a rat, for instance, the finding of its way through a maze is not so much a departure from the normal as something entirely unknown, though it is, of course, true that the ability to do so might well prove valuable.

Perhaps the difference between the two kinds of behaviour can be brought out most clearly by describing a series of actions involving both. It is a very remarkable example, one that has been referred to frequently in books on animal behaviour. Another point in its favour is that though the learning part of it involves an artificially imposed experiment, it was carried out

in the field. The actor was a hunting wasp of the genus *Eumenes*, and the observations were recorded in India by Hingston. This wasp builds little pots of clay, which she then stocks with the inert bodies of caterpillars, on the top of which she lays an egg. When the larva hatches from the egg it feeds on the caterpillars. Hingston made the experiment of waiting until *Eumenes* had begun carrying caterpillars and then made a hole in the bottom of the clay pot. The first caterpillar fell through the hole, but the wasp took no notice and went on with her provisioning. The second caterpillar hung half-way out, but still *Eumenes* carried on, so that later caterpillars remained inside. It was only then that she seemed to realize that something was wrong and set about putting it right. She managed to push the protruding caterpillar back through the hole, but only after a long and painful effort. She then flew away, returned with a pellet of clay and patched up the hole. In a second example, involving another wasp, this time a hunter of spiders, when a hole was made it was again repaired, but there was a further departure from the normal. In the ordinary way, when the pot has been stocked, the wasp closes it with clay working from the outside. But this one, before repairing the hole, appeared to hesitate as to which method she should use, and finally decided to repair it from within.

Now in these examples the whole business of building the pot, stocking it with food for the larva, laying the egg, and finally sealing up the pot, is instinctive, an inherited and fixed chain of actions or pattern of behaviour peculiar to the species. The rest of it, namely noticing the damage, stuffing the caterpillar back, and repairing the hole, has every appearance of an intelligent process, what psychologists call insight learning, something more advanced than trial and error. We might expect such adaptability to abnormal circumstances in a dog or a bird. In a wasp it is very remarkable. But can we be quite sure that it was something outside the normal experience of these insects?

Wasps of the sand-pit

The amateur naturalist interested in the behaviour of animals is unlikely to see anything as remarkable as this, but is certain on the other hand to find a great deal of quite absorbing interest. Apart from the hunting wasps, which have received a good deal of attention from the time of Fabre, the field of insect behaviour is only partially explored. Much has been learned about birds, a little about mammals, but there remains almost unlimited scope for an inquirer. The pursuit is not without its vexations. In the first place a vast amount of patience is essential, long periods of waiting for something to happen, for a wasp for instance to return from a foraging expedition, or to emerge from her nest-hole. Then there is the experience, certain to recur many times, of entering the theatre long after the rise of the curtain on the beginning of the performance, or of seeing it broken off for no apparent reason just as the climax is about to be reached.

The result, as in my own case, is apt to be a series of note-books filled with fragmentary and inconclusive observations. The taking of notes in the field is of vital importance, but for all that is a practice easily overdone. The beginner, rightly mistrustful of his memory, is much inclined to do his watching notebook in hand, to scribble furiously and illegibly, and in doing so to miss some critical link in the chain. The only possible course in these circumstances is to continue to collect fragments however inconclusive and even contradictory they may seem, and to trust in one's subsequent ability to join the fragments together into some sort of comprehensive whole, so that conclusions, whether new or old, will be arrived at in time.

As evidence both of these difficulties and of the absorbing interest of the pursuit, certainly in no way because of their originality, I offer some of my own experiences. The scene is that abandoned sand-pit described in a previous chapter, where for once human activity, instead of destroying animal life, has provided in this instance tall cliffs of compacted sand exactly suited to the requirements of sand-martins and of a host of

insects, including several species of hunting wasp. Notable among these, though by no means common, is *Priocnemis exaltatus*, a spider-hunter little more than half an inch in length, black but with a patch of chestnut on her abdomen. Her specific name is derived from the furious energy, the desperate air of having not a moment to lose, with which she goes about most, though not all, of her business. My first introduction to her was at the time when she was filling up and removing all trace of the burrow in which a paralysed spider had previously been stowed away as food for the offspring she was never to see. This masking of the burrow is very important because of the parasitic insects whose concern it is to profit from the work of others by laying an egg, so that the larva hatching from it will devour the spider intended for the larva of the wasp. There is one great advantage in observing insects as opposed to birds. The inquirer can obtrude himself so thoroughly as to gaze at a range of inches and even bring a lens to bear, and they will remain serenely oblivious.

The filling up and masking of the hole occupied my *Priocnemis* for nearly half an hour of dedicated labour. A greater degree of methodical thoroughness would not have been possible. At first I could see only her head and thorax protruding from the hole, as with her mandibles she drew sand-grains towards her so that they filled up the hole. When she had filled the hole almost to the level of the surrounding sand, it was possible to take exact note of her method of working. The mandibles and foremost pair of legs were used to rake in more grains of sand. That was one phase lasting for three or four minutes, and it alternated with another which was the pressing down of the grains with movements of her abdomen. Before long all trace of the hole had been obliterated, but she was not yet satisfied and the raking and ramming went on. At last it was done, the alternating phases came to an end, and there began a different phase of walking slowly round in a last inspection. Wings and antennae, hitherto inert, resumed their normal incessant quivering. After one final intent scrutiny she was gone.

Later, on more than one occasion, I was to see the digging of

the burrow, but this was bewildering, for it consisted of furious digging, when *Priocnemis* was frequently upside down in the hole with forelegs and mandibles frantically working. But the hole would be dug to a depth of no more than a few millimetres only to be abandoned as though it were in some way unsuitable, and she would begin all over again somewhere else. That was the abortive beginning of the drama of which I had previously seen only the last act. On yet another occasion, and again more than once, I watched the second act, when a wasp, having prepared a hole, had just caught and stung a spider. This inert burden, fully as big as herself, she proceeded to drag towards the hole in an undeviating line, under and over the most formidable obstacles in the form of entanglements of grass-blades, or mountains of pebbles piled in her path. It is supposed that this is done by memorizing the route, often several yards in length, by recognition of landmarks. But I have watched *Priocnemis* dragging her prey on several occasions, as well as another species, *Pompilus nigerrimus*, with similar habits. Invariably they walked backwards all the way, which would seem to make recognition difficult.

Once, on a memorable occasion, I watched *Priocnemis* making her way backwards undeviatingly, dragging a spider for a distance of more than five feet up the vertical and sometimes overhanging face of the sand-pit, only to miss her footing and roll from top to bottom of that vertiginous precipice. I found her at my feet among leaves of coltsfoot, and the spider was still firmly in her grasp.

On this occasion I had seen the wasp, before she began dragging the spider, spend several feverish minutes inspecting a number of holes dug not by herself, but by a different and much commoner species. This was *Mellinus arvensis*, a fly-hunter of a kind that makes no attempt at masking the entrance of its burrow. Since these are invariably hollowed out in the vertical face of the pit, any attempt at masking would be futile, since sand scraped would at once trickle to the floor of the pit. It was clear that in this instance *Priocnemis* was making use of an abandoned *Mellinus* burrow. After inspecting three or four,

she signalled her choice of one by spending a good twenty minutes out of sight inside. On that first ascent of the precipice which had ended in disaster, she had dragged the spider past this hole of her choice and continued climbing to a point twice its height above ground level. Now, before making a second attempt, she made a second inspection of *Mellinus* holes, again chose one of them and again spent twenty minutes or so inside. This preparation completed, she came back for her spider, abandoned meantime among the coltsfoot plants, overshot it by half an inch, turned, found it and laid hold of one of its legs. Then the fringe of the coltsfoot jungle had to be traversed. This she did without slackening speed, under and over the broad discs of the leaves. More than once she took flying leaps, still clinging fast to the spider. Most remarkable of all was the way she negotiated a foot-long stretch of coltsfoot stem drooping in a shallow, horizontal arc in the direction she was taking. Along that elevated board-walk she sidled unhesitatingly crab-wise, using so far as I could see her middle and hindmost pairs of legs, while head and thorax, together with the body of the spider, hung over the abyss some eighteen inches below.

Then came the sand-face and at last the hole. But to my surprise she seemed to have forgotten all her previous preparation, and set to work trying to drag the spider into another, smaller hole close by. It was too big to go in. This seemed to upset her completely. Leaving the spider precariously balanced on the vertical sand-face, she began scurrying anxiously from one hole to another, including the right one more than once, covering a space with a radius of three or four feet. But I must cut this story short. The spider fell down again amongst the coltsfoot. There was a third preparation of a hole, a third retrieving of the spider, and a third ascent of the precipice, before with one more false move, at last she succeeded in stowing it safely away. What a strange combination of skill, resolution, and what appeared to be sheer muddle-headedness. The whole procedure, I may add, occupied the greater part of an afternoon in late August.

Theory of releasers

Of the examples of behaviour given so far, that concerning the wasp *Eumenes* was a remarkable instance of adaptability to what seemed to be abnormal circumstances, of the flexibility of a chain of instinctive acts. It was a combination of instinct and learning. My *Priocnemis*, on the other hand, exhibited a wealth of instinctive behaviour, but precious little adaptability. Her behaviour was decidedly inflexible, if those odd 'mistakes' of hers are to be construed as such. In what way the abnormal was introduced, if at all, it is very difficult to say. But there is no doubt that inflexibility is more commonly observed than the opposite. A spider, for example, spins her web on a foundation of radii, like the spokes of a wheel, stretching from the hub to the circumference. Making use of these radii, she lays down spirals at right angles from one of them to the next, outwards from the hub. If some of the radii are severed while she is still at work on the spiral, she makes no attempt at repairing the damage, but goes on with what she is doing, with the result that the spiral, lacking its needful support, sags ridiculously in places, and the web spun by this rigidly predetermined chain of actions has the appearance of having been absurdly botched.

This inflexibility is so frequently seen in instinctive behaviour that it can be said to be typical, and this is only one of a number of features not so much typical as invariable. Another feature is that instinctive action of a peculiar kind is inherited and as characteristic of the species of animal in question as its anatomical structure or coloration. A third, and in some ways most important of all, is that each component of the chain, each unit in the pattern, is called forth by some item of the environment, whether for instance a food-plant or a member of the same or of a different species. It is a matter of receiving a signal and responding by giving one of its own, or as students of animal behaviour say, of an action being released, set off, by a stimulus known as the releaser.

Thus the releaser required to stimulate the aggressive

behaviour of a male stickleback is the patch of red displayed by another male stickleback, that required to release the act of leading a female to the nest, where she is to lay her eggs, is her belly swollen with the same eggs and protruded appeasingly and invitingly in a submissive posture before the male. Among birds a well-known example is once more the colour red on the breast of rival male robins, though here both sexes are so ornamented. The sight of this releases chasing away of the trespasser-robin by the lord of a territory. Now in these and other examples it has been proved conclusively that it is the one simple feature that matters, the two mere facts of redness, the one mere fact of a swelling on the underside. A male stickleback will attack the crudest model provided it has a patch of red in the right place. The same stickleback will attempt to lead to the nest a mere vaguely fish-like lump representing the female provided its belly protrudes. A male robin will attack a mass of red feathers devoid of head or legs. In each of these examples, moreover, a model accurate in every other respect, but lacking the one significant feature, elicits no more than a faint response. It is a matter then of sensory stimuli given out and responded to.

In the examples cited the stimuli are all visual, evidence that in the stickleback and the robin sight is one of the more important senses. But the stimulus, the releaser, could equally well be associated with hearing, smell, touch, or even some vaguely understood chemical perception, vaguely understood that is to say by the human observer, not by the creature concerned. It is important to understand also that, while these examples each consist of a single releaser and its corresponding response, an elaborate and continuous pattern of behaviour is made up of a series of them, each following and consequent upon the one before, a sort of chain reaction culminating in an act, such as mating or the laying of eggs, which is the consummation of the whole series. It is not necessary for each link in the chain to be responded to by the same sense. In the stickleback's pattern of behaviour, for instance, most of the releasers are visual but not all. We would not expect hearing to play a part where stickle-

backs are concerned, but at least one other sense takes part. When the female stickleback enters the nest, having first been shown the way by the male, she requires a fresh releaser to induce her to lay her eggs, and this is given by the male who hovers above her and prods the base of her tail with his snout. We know that this is a tactile stimulus because it is possible to produce the same result with the end of a glass rod. To single out another unit of the same stickleback pattern, after the laying of the eggs and their fertilization, the male begins upon his arduous duties of keeping them oxygenated by winnowing the water above the nest. In this case the appropriate releaser is given out by the eggs, either by scent or by some chemical means.

General theory of behaviour

The theory of releasers, significant as it is, goes only part of the way towards explaining the behaviour of animals. It is in fact no more than a part of a general, comprehensive theory. What was needed was something to explain not merely signals and the responses made to them, but something also of the internal conditioning of the animal, which makes it responsive to stimuli. This might explain instinctive behaviour, but leaves out of account the part played by learning, that adaptability to unusual or changing circumstances which on occasions gives flexibility to some part of a chain.

Such a comprehensive theory we now have and it is mainly the work of two men, Konrad Lorenz, author of *King Solomon's Ring*, and N. Tinbergen now of Oxford University. According to this theory the characteristic action of an animal has three essential and consecutive components. First there is the build-up, mainly within the animal, of that nervous and physiological condition of excitability, or as we say when speaking of human beings, of a state of emotion. This is thought of as energy accumulated under some sort of pressure, so that the animal is compelled to give expression to it. It may be a matter of hormones liberated into the blood-stream, bringing about the urge to

perform the act of mating, but this is only one example. This part of the process has been given the name of the reaction specific energy, and the word specific is important, implying as it does that the energy accumulated at any one time leads to one particular and characteristic reaction only.

That is the first component or phase, and the second follows at once, for provided the pressure is sufficiently great it causes movement on the part of the animal, the initiation of a fresh phase of a length varying according to circumstances, during which the animal is in search of the opportunity to bring its reaction specific energy into play. The movement is either random or directed, short or comparatively prolonged; and it is during this phase alone, known as that of appetitive behaviour, that adaptability to circumstances or learning is exhibited. The phase of appetitive behaviour, that is to say, can be modified as a result of the learning ability of the animal, so that the goal, which is the third phase, is reached correspondingly more quickly or more easily.

Now, provided conditions are the right ones, comes the third or consummatory phase, and now also comes the releaser and the response to it. The one is involved in the other, for without the releaser there can normally be no consummatory act. The necessary conditions for calling it forth are in fact two: the reaction specific energy must be at the required pitch, and the needed releaser, as for instance the red breast of the rival male stickleback or the swollen belly of the female, must be present to call forth the act of consummation. One other point is important. The consummatory act, once performed, will use up either a part or the whole of the reaction specific energy. If it is all used up then the act cannot be repeated until it has once more been stored up. The simple parallel of a bath from which the plug has been removed suggests itself. The bath must be filled up once more, but in an animal, unlike a bath, while this inflow is in operation there can be no outflow. But a repetition of the consummatory act can be induced either by a repetition of the releaser at a greater intensity than before, or possibly by a different releaser. Lorenz, for instance, could induce young jack-

daws to fly up from the ground by raising himself sharply from a squatting posture, but if he wanted to make them repeat the movement, had to take quick steps away from them. It is also true that there is such a thing as a consummatory situation rather than a consummatory act. A familiar example is the behaviour of a kitten in a new home, immediately embarking on a detailed exploration of an unfamiliar room. This is appetitive behaviour called forth by the stimulus of fresh surroundings, and it leads in time to a consummatory situation of familiarity with the topography of the room, which in the wild state, or even a domesticated one, will be of future value to the kitten.

All this, that is to say the three phases, must be thought of, not merely as comprising a single action, but also as units of such a complicated pattern of behaviour as nest-building or web-spinning, or to return to the stickleback, of the whole chain of its breeding behaviour, each link in the chain involving a renewed storing up of reaction specific energy, renewed appetitive behaviour, a renewed releaser of the same or of a different sort, and a renewed response.

This is interesting and comprehensive enough, but the great merit of the theory is that it does so much to explain, not only instinctive and learned activities of what may be called the normal kind, but also certain complications involving actions that without it are entirely inexplicable, that previously in fact seemed to make no sense at all. What are we to think for instance of a young bird that goes through all the motions of catching and eating insects that are not there, or of a stickleback that spends time and energy winnowing a nest in which the eggs have not yet been laid? The first of these is accounted for within the framework of the theory by supposing that in this young bird the reaction specific energy is at such high pressure that it bursts its bounds even if there exists no releaser in the shape of a moving insect to bring this about. This has been called a vacuum or overflow reaction. It will probably occur to the reader that another theoretical explanation would equally well account for the facts, namely that some sort of releaser is in fact

present, but is recognizable by the animal only and not by the human observer. This is the explanation favoured by some authorities.

DISPLACEMENT ACTIVITIES. The other anomaly, that of the stickleback fanning non-existent eggs, resembles the last outwardly but is explained in different terms, also within the framework of the theory. The important point to understand here is that the fanning is being done at the wrong time, rightfully belongs to a stage further on in the pattern of behaviour. When the male stickleback turns away from a courted female to lead her to the nest, he 'expects' her to follow. If she does, the rest of the pattern continues on its appointed course. If, as quite often happens, she fails to do so, then that portion of his remaining reaction specific energy finds expression sometimes in a repeated attempt to induce her, but on other occasions in an act belonging to that part of the pattern following upon the laying of the eggs. But in this case no eggs have yet been laid, and the result is an apparent absurdity. The male stickleback has in fact jumped or sparked over from one part of the pattern to a later one.

These displacement activities, as they are called, occur very frequently in the behaviour of animals, and are not unknown among human beings. It will be worth while giving a few more examples, and one of them can be taken once more from the stickleback. When on the boundary between two territories rival males confront one another in a bellicose manner, one will usually attack, but on occasions his aggressiveness takes the form not of attack but of display. He upends himself with dorsal spines directed towards his rival and snout prodding into the sand on the floor of the aquarium. That also is an action performed in the wrong context, for it is properly a part of the act of making a nest. The cause of it may be that he has failed to receive the appropriate response, the answer to his challenge. from the other male. But there is another, and perhaps likelier, explanation, that it is the outcome of what is known as ambivalence. That is to say he is under the stress of two conflicting

drives, the drive to attack and the drive to retreat. The result of being thus pulled at the same time in two directions is a compromise which gives an outlet, though a displaced one, to his reaction specific energy.

In a similar way, when two oystercatchers are squaring up to one another, one will suddenly break off his display and tuck his bill into the feathers of his back, going through the motions of falling asleep It is a sort of token sleep, a displacement sleeping, and it is important to realize that it is no more than a token, a pretence, an act performed out of context. Again, of two herring-gulls disputing ownership of a territory, one will suddenly begin pulling vigorously at a tuft of grass. This is another displacement activity belonging, like the upending of the stickleback, to the context of nest-building. Yet another form frequently seen among birds, particularly perhaps ducks, is displacement preening, a mere touching of the feathers behind the head with the bill. This example is specially interesting, for it often becomes part of the ritual of courtship.

Courtship

The last sentence brings in one of the most important of animal activities, those preliminaries to mating, often elaborate and ritualized, which we call courtship. Because some form of courtship is indulged in by almost all animals in which the sexes are separate, and because it so vividly illustrates many of the principles of animal behaviour, some reference to it here is inevitable. Some writers would be inclined to give it a chapter to itself. Yet another reason for giving it prominence is its relationship with certain displacement activities.

Since courtship is so widespread among animals and often so elaborate, it follows that it must have considerable biological significance, and there is no doubt that it justifies itself abundantly. Its main purpose in the scheme of things is to effect a timing, a synchronization. Males and females must arrive at a condition of readiness for mating at the same time. This of course is largely a physiological matter, the ripening of the male

and female gametes, but it can be assisted and stimulated by various types of behaviour. Of these the most elementary, and the first to occur, is some kind of movement to the breeding-ground, if there is a special one, in the spring, so that the two sexes may expect to meet. This is synchronization of a sort, but is no more than approximate. Males and females are roughly in the same place at the same time. That is a beginning, of which the end is the physical act of mating. In between lies all the rest of the pattern of behaviour, of which something has been said already. The further degree of synchronization, the preliminaries to mating, is a matter both of persuasion and appeasement, and the reasons for these being necessary are worth explaining.

As I have said at some length already, all animals are subject to social appetite, tend readily to associate in groups or demes of the same species with a varying degree of integration. But mating means more than this. It means physical contact of the most intimate kind. The only other occasions when physical contact occurs to a comparable extent is when a predator is devouring its prey. Consequently it is not too much to say that physical contact is apt to be associated, though not of course consciously, with danger. To this it can be added that both during courtship and still more in the act of mating, both animals are in a helpless condition. It is not surprising therefore that there should exist this strong element of appeasement, that a certain reluctance should show itself, which has to be overcome. This reluctance, which could well be called coyness, is more likely to be shown by the female than the male. The female carries the eggs, both before and after fertilization when that takes place internally, is called upon to lay the eggs, and after that plays in most cases a more notable part in care of the young. It can be said therefore that the female is the more biologically valuable of the two, and it is more often the coyness of the female that has to be overcome. On the whole therefore it is the male that does the courting, which to so great an extent is this overcoming of reluctance. Most people would be likely to say that the male shows no reluctance, but that is not always true.

Even he, in many instances, shows if not coyness at least that ambivalence of attitude to which I have already alluded.

But of course it is true that on the whole the male shows more eagerness than reluctance, and there is appeasement of another kind to be taken into account. The truth is that the males of very many species are extremely pugnacious during the breeding season, and that this pugnacity is directed not only against rival males, but against females as well. For this reason the female is frequently much put to it to appease the hostility of the male, so that she shall be courted rather than attacked. Here, as almost everywhere else in animal behaviour, we see releasers at work. At first the presence of the female often releases attack in the male, and this among sticklebacks takes the form known as the zig-zag dance, a to-and-fro movement, alternately towards and away from the female. This is an expression of ambivalence on his part, but the drive of sexual eagerness overcomes the drive to retreat, which means that appeasement is called for. The female thereupon adopts a submissive posture, head up and tail up in a way that presents her swollen belly. This, as we saw, is also a releaser, and it elicits the sex drive at full strength in the male, so that he turns and swims at flashing speed to the nest, while that in its turn releases a following response from the female.

The act of appeasement on the part of the female stickleback is associated with fertilization that takes place externally. Among birds fertilization is internal, requiring copulation, and so the hen bird's act of appeasement takes the form of a crouching attitude, a direct invitation to mount. Among spiders there occurs a highly interesting reversal of this procedure, since among them it is often the female that is aggressive, sometimes so much so that the approach of the male involves him in danger to his very life, and accordingly it is he who does the appeasing. He sways his body from side to side, and at the same time waves his palps in a sort of semaphore message to the effect that his intentions are wholly amorous.

The releasers in these examples are visual, and since most animals are near-sighted, they are those concerned with the

immediate preliminaries either to internal or external fertilization. Hearing and scent on the other hand operate at greater distances, besides being senses very highly developed in many animals of widely differing relationship. We would expect therefore to find them made use of to bring the sexes together, sometimes from an astonishingly great distance. Among auditory releasers of this kind is the song or the call-notes of birds, the croaking of frogs, the stridulation of grasshoppers and crickets. Many of them serve a double purpose as warnings or challenges to rival males, and as invitations to potential mates. Scent is widely used, and we find some very remarkable examples among insects, particularly some of the moths. The oak-eggar (*Lasiocampa quercus*) is perhaps the most striking example. The males have feathery antennae which are so sensitive that they will respond to the scent of a female distant from them a mile or even more. They will even invade towns in their quest, where all kinds of other scents might be expected to overcome the infinitesimal, probably molecular, trace of the females. In certain other moths it is the male that produces the scent, when at close quarters with the female, and so induces her to mate.

This bringing together in time and place is the chief function of courtship, but there is another and entirely different one, applying not to the thing as such, but to the methods by which it is carried out. I referred to it in Chapter 8 in connexion with evolution. This is that reproductive isolation between species, that barrier which prevents attempts at mating between animals of different kinds. As we saw, there are several of these barriers, and one important one is that patterns of breeding behaviour are as characteristic of the species as its structure and appearance. In other words it is not merely a matter of signals and responses, but of the right signals and responses. It is here that we can appreciate the importance, and therefore the existence, of releasers and responses being arranged in chains or patterns rather than existing singly. A single releaser might evoke the appropriate response, but it is exceedingly unlikely that this would happen when there is an ordered chain of consecutive

links. At least one of the links in the breeding behaviour pattern of two species will be different, and this will be of particular importance in the case of two closely allied species. For instance there are two distinct species of stickleback in British waters, the three-spined which is the common one, and the ten-spined. There is considerable similarity in their breeding behaviour, but whereas the male three-spined wears a wedding garment of red and blue, the ten-spined wears one of sober black. As a result it would be highly unlikely for a female three-spined to respond to the advances of a male ten-spined. Again, in studying the breeding behaviour of the grayling butterfly, Tinbergen found that males would pursue, not female graylings only, but other butterflies also, in fact almost any small creature that moved through the air. Flight was the releaser and it elicited pursuit on the part of the male grayling. But the next link in the chain, the subsequent releaser, had to be shown and this was done by the female who soon came to rest. Only then could courtship proceed according to plan, the specific plan of the grayling. For this reason grayling butterflies seldom go far in their attempts to mate say with meadow browns.

This brings me to a particular kind of visual releaser and back to displacement activities, for there is one of these, displacement preening, which is known to function as a releaser with an importance of its own, has become something more, that is to say, than a display of nervous tension, which is what all displacement activities in origin are. There are, as we saw, a number of these irrelevant activities – feeding, sleeping, and so on but this displacement preening has been, so to speak, picked out by natural selection from the others and brought into close association with a releaser that plays a prominent part in the courtship ceremony of certain birds, particularly wild ducks. With a great many birds an important part of the ceremony is the display of some conspicuous feature in the plumage, some gaudy scheme of stripes, a boldly-marked circle or 'eye'. During courtship this part of the plumage is often raised, pushed forward, made the most of in some other way. But in the garganey drake for instance there is more. The wing is not

merely raised so as to display to advantage the vivid grey-blue of the wing-coverts, but at the same time is lightly touched by the bird's bill in an abortive, token preening movement. This is secondary to and associated with the raising of the wing, drawing additional attention to it. What was originally the result of nervous tension has been formalized so as to become part of a ritualistic act. A displacement activity has become a releaser, or a significant part of one. This and other examples of the same thing have led to a belief that the origin of releasers is to be found, partly at least, in displacement activities.

Another and related effect of natural selection is worth mentioning here in connexion this time with facial contortions, which are the outcome of nervous excitement. We might very well call them expressions of emotion. Such are the gaping of the male stickleback; the bristling hair, the snarling grimace, the glaring eyes, of many of the larger mammals. These, in origin by-products, have acquired survival value in the course of ages because of their usefulness in threatening displays against rival males.

A word of caution must be given here concerning almost all that has been said about instinct and learning. The theories propounded, the explanations given are highly interesting and the outcome of comparatively recent research. They can be accepted as well-founded, but it would be a mistake to look upon them as comprising the whole truth, and it is sound procedure to criticize them as being too mechanistic in their interpretation of animal behaviour. They are in fact open to criticism in much the same way as was done in the case of the singing of birds in Chapter 4, when territories were under consideration. These very illuminating theories were to a large extent propounded as a reaction to earlier attempts at explaining the behaviour of animals, which failed because the problem was approached in too subjective, too anthropocentric, a spirit. The earlier investigators tended to interpret the activities of animals along the lines of human activities, and there is reason for supposing that, as so often happens, the reaction has gone too far. Animals are not governed by promptings parallel with those of human

beings, but on the other hand neither are they machines, responding wholly and fixedly to machine-made stimuli or releasers. They must be thought of as beings endowed with some degree of initiative, of volition. Also, each one is an individual in its own right, which means that one stickleback must not be expected to behave in exactly the same way as another stickleback, nor one robin invariably after the fashion of another robin.

Further examples of animal behaviour

Ideally this chapter should include a representative account of the behaviour of animals, both instinctive and learned, ranging from the protozoa and ending with the higher mammals. Considerations of space forbid any such thing, but I cannot go on to another subject without giving a highly selective description of some of the more interesting examples, acknowledging at the same time my indebtedness to Dr W. H. Thorpe's book, *Learning and Instinct in Animals*.

INVERTEBRATES. Instinctive behaviour, and sometimes what looks very like the result of learning, is easily demonstrated among creatures as low in the scale of development as the one-celled protozoa. *Amoeba* for instance, one of the best known, moves by protruding what are known as false feet, which are in fact lobes of its own jelly-like substance, and then drawing itself in that direction. When confronted in the laboratory with a lighted area, it reacts negatively with regard to the light, withdrawing an advancing lobe and protruding one on the opposite side, so that in effect it retreats from what it appears to recognize as a hostile environment. Another protozoan, the ciliated *Paramoecium*, is capable of exercising what looks uncommonly like choice between particles suitable for food and others that are not.

Certain sea-anemones show clear evidence of that form of learning known as habituation, failing to respond after a time to mechanical disturbances in a way that shows that this is not

merely a matter of fatigue. In one series of experiments one of these creatures was presented with a ball of absorbent paper soaked in fish-juice. At first this was accepted, but repeated offers resulted in refusal. This gives the impression of memory, connecting one set of conditions with another that brought unpleasant consequences. Another and perhaps more striking example was shown by a species of flatworm which when exposed to light immediately seeks out the cover of darkness. This happens in its natural environment, the sea-shore, when the stone under which it is hiding at low tide is overturned, and the animal makes for another. In the laboratory it was placed in a dish, and when a light was turned on it at once began to move away. Now if another and opposing stimulus is applied, such as touching its forward end, movement stops. In the experiment this touching was done repeatedly as soon as the light was turned on, with the result that after several repetitions the worm seemed to associate the touch, which prevented movement, with the turning on of the light, which normally elicited movement, so that when the light came on it stayed still.

It seems that habituation has established itself very widely, if not universally, among animals, and it is not difficult to see why. What it amounts to is the ability to learn by experience which of the stimuli that life subjects them to are of importance and which are not. Significant ones will evoke a response, insignificant ones will be ignored. All small, defenceless creatures must be alive to possible dangers of a wide variety, constantly on guard against any moving object, and in fact any strange and sudden disturbance of their equanimity. But life would be unendurable if any and all of these were to cause automatic responses in the way of some sort of avoiding action. The ability to learn therefore comes to the animal's aid, giving it the power to discriminate between harmful and harmless disturbances.

The great phylum of the arthropods is not merely that which comprises the largest number of species: it contains many more species than all the others added together. Of these, insects provide the great majority. More than half a million have

been described and each year adds to the total. A leading authority has estimated that there may well be something like two and a half million kinds of insect in the world, ranging from primitive forms of microscropic size up to the Hymenoptera (ants, bees, wasps, and their allies), some of which can be regarded as on a par with birds and mammals in specialized structure, and well above them in complexity of behaviour What behaviour could be more complex, indeed well-nigh incredibly so, than the now fully recognized dance of the honey-bee in the darkness of the hive, passing on to her companions the direction and the distance of a newly discovered source of food?

We are much inclined to think of the use of a tool as a faculty distinguishing man from other animals, that it was this specialized skill, perfected by palaeolithic man with his implements of chipped stone, which helped materially to accelerate his evolution From this we would conclude that any animal known to use anything remotely approximating to a tool was a very remarkable animal indeed, showing what can only be described as insight learning Yet there are a few tool-using animals and they are known chiefly among the arthropods Which is the more remarkable, the use of a living or of an inanimate tool? There are examples of both. The crab *Melia*, referred to in an earlier chapter, which uses sea-anemones as food-catching appliances, is an example of the former. The anemones are held in the crab's pincers, and the tool-user abstracts the food it needs from among the tentacles of the anemones by means of its foremost pair of legs There are tropical ants that make use of their own larvae as living sewing-machines to sew leaves together as shelters. The material used is the silk secreted by the larvae, and the ants hold them in their mandibles so that the stitching can be performed.

As for users of inanimate tools, and these after all are the kind favoured by human beings from palaeolithic times up to the present, the most famous example is the hunting wasp *Ammophila* which was seen by the American naturalists, the Peckhams, to bring into play a rammer in the form of a small pebble, with which to press down the soil over the mouth of her

completed burrow. This was observed, not as the usual practice of all *Ammophila* wasps, but as the achievement of a particular individual, a sort of genius among wasps, blazing a fresh trail. But it seems that this is too romantic a view. The same thing has been seen since among members of the same notable genus, but more as the established custom, not the startling innovation of an outstanding personage. Dr W. H. Thorpe indeed, in his recent comprehensive study of animal behaviour, is much inclined to deny that it is an example of insight learning at all, and to regard it, rather disappointingly, as a natural outcome of manipulation of clods of earth in the course of obliterating the entrance to their burrows. He prefers to think of it as trial and error.

VERTEBRATES. Coming to the vertebrates, we find several striking behaviour patterns among fishes. Few would regard them as creatures endowed with even the rudiments of intelligence, and yet there is one, a species of goby known as *Bathygobius soporator*, inhabiting tidal pools, which appears to be gifted with memory. At low tide this fish has a way of jumping from one pool to another and of skipping over wet rocks separating pools. It is of course of the utmost importance that it should know the right direction for jumping or skipping, so as to avoid finding itself stranded in some dry cranny where it would in all probability die. Experiments have established the fact that this is not because it can look before it leaps. Nor is the method orientation to the sun, or even trial and error. The one conclusion that fitted the facts was that *Bathygobius* was accustomed to swimming over the pools when the tide was in, and having done so, was able to remember the general arrangement of the pools, and so to jump or slither unerringly from one to another when the tide had ebbed.

Enough has been said about the three-spined stickleback, with its complicated pattern of breeding behaviour and its strong attachment to territory, to emphasize that it is something of a star performer, at least where instinctive behaviour is concerned. But it is by no means alone in these respects, and the

defining of territories is a well-established custom among fresh water as well as marine fishes. Several of the tropical Cichlids have been intensively studied with highly interesting results, throwing light for instance on the evolution of releasers. Earlier in this chapter I pointed out how some of these can be shown to have developed in all probability from displacement activities. Study of the Cichlids makes it reasonably clear that many releasers are no more than movements of everyday life made more emphatic. This applies particularly to the beginnings of the movements, which are frequently left incomplete and are then known as intention movements. Among birds, for instance, a common intention movement, signifying flight, is a sudden crouching. Among these Cichlids, some when about to move make a sideways swing of the head, together with a furling of one of the dorsal fins. In some kinds of Cichlid this intention movement has become an important releaser responded to by the swarm of young, which wheels in the direction indicated by the swing of the parent's head In others it is the fin movement that evolution has singled out, and the effect is emphasized by a row of coloured spots along the spines which flicker as the fin is raised and lowered. One of the Cichlids has shown that it is capable of benefiting from experience. A male brought up in isolation will be deceived by a simple model of a female, but one brought up in the company of females can recognize a dummy for what it is.

Behaviour patterns among birds are so varied, from the one extreme of the apparent absence of any courtship at all, to the other of the breath-taking displays of the birds-of-paradise, as to make this an exceedingly worth-while study in itself. In between those extremes lies an infinity of gradations, each differing in some respect from all the others. There are birds in which the sexes are outwardly alike and courtship mutual, with comparatively little aggressive display between males; others in which, though the sexes are equally indistinguishable, as among robins, courtship is negligible, but rivalry between males intense and prolonged; others again, such as pheasants and ducks, where sexual dimorphism is so marked that cock and hen

are scarcely recognizable as belonging to the same species. There are a few, like the red-necked phalarope of Hebridean lochans, in which the hen is more gaily coloured, while the cock resembles the stickleback in taking upon himself all the duties of parenthood.

Consider the great crested grebe (Plate 7a), so much commoner today on our inland waters and flooded gravel pits than twenty-five years ago. The sexes are outwardly almost indistinguishable, and courtship displays correspondingly reciprocal, varying from the frequent head-shaking ceremonies to the presentation of beakfuls of weed to one another, to mention only two out of several. It appears though that these displays which may begin as early as January, are not really concerned with courtship as such, in the sense of being immediate preliminaries to mating. There is another and later set of ceremonies, quite distinct, taking place always on the platform of weed which is to be the nest, and leading directly to coition. The first set seems to be concerned only with appeasement. There is also their charming habit of carrying the chicks on their backs often dividing the brood between father and mother. This carrying of the brood is an adaptation made necessary by the voracity of carnivorous pike which are the grebe's chief predator so long as they are chicks. But it is pleasant to know that the parents go some way towards restoring the balance by feeding their young on the fry of the pike as well as that of other fish.

Mention of the chick-carrying habit of the great crested grebe brings to mind the behaviour of birds connected with care of their young. Where this duty is concerned birds can be divided into two classes: that in which the young remain for some time in the nest (Plate 8), completely dependent on their parents for food and warmth; and the other in which the chicks are able to run about almost from the moment of hatching (Plate 7b). Broadly speaking the difference corresponds to that between tree and bush-nesting birds on the one hand, and ground-nesters on the other, though the correspondence is not quite complete. Adaptations and behaviour differ widely from one class to the other. What contrast could be greater, for

example, than that between the naked, helpless, and in our eyes repulsive chicks of the blackbird, and those of the ringed plover, charming little animated balls of down, fully clothed, cryptically coloured, and capable of running like mice when the shell of the egg has only recently been cracked. Corresponding adaptations of behaviour govern the lives of these widely contrasted chicks, controlled by utterly different releasers.

The adult blackbirds spend the greater part of their time finding food for their young, and when this is presented to the chicks the releaser in constant operation is the physical disturbance of their alighting on the rim of the nest. To this the chicks instantly respond by a wide gaping of their bills, a movement that can be induced by the touch of a human hand. But that is too simple a statement to cover the facts. When the nestlings hatch they are blind for some days, and it is then that gaping is evoked by the movement of the alighting parent, the yawning bills directed vertically upwards. As soon as the eyes open the chicks are able to respond to a visual releaser, that is to say no longer vertically upwards, but at an angle towards the parent, not just at once however. A short intermediate phase intervenes, when though the response is made to a visual releaser, it is not yet directed by it, with the result that the gaping is still upwards in spite of the fact that they can see. After that they gape in the direction of the parent's bill with its proffered food.

It is perhaps a little surprising to learn that the parents of these nest-dwelling young require a releaser no less than their infants. This is provided sometimes by a vivid colouring of the inside of the throat of the young bird, sometimes by a wide pale-coloured flange round the base of the bill, a feature that disappears with infancy, and applies particularly to birds that nest in semi-darkness, such as the starling. In some species, such as the reed-warbler, the hawfinch, and the bearded tit, the inside of the young bird's throat is ornamented by a conspicuous pattern of stripes, triangles, or spots serving to guide the parent's bill not merely to the gaping mouth, but to the exact spot where the food must be inserted. In one tropical finch, which nests in the dark, the throat of the nestling is

equipped with spots deserving to be called luminous, since they reflect what little light there is. Directing patterns such as these provide a most interesting parallel with the honey-guides in the form of converging lines on the petals of flowers intended to guide bees to the nectar within.

I cannot pass over one other and rather delightful instance of cooperative behaviour on the part of parents and chicks, though the subject is not usually classed as delightful. This is the neat system of nest sanitation. The young birds do not foul the nest indiscriminately. What happens is that the adult bird waits beside the nest after presenting food. Presently one or other of the chicks begins to squirm, rolls to one side and extrudes its faeces enclosed in a tiny white bag. This is either devoured by the parent or carried away and dropped some distance from the nest. The releasers here seem to be, for the young bird, the continued presence of the parent, and for the parent the conspicuous whiteness of the faecal sac. How so dainty a device came to be evolved is something of a mystery, but at least its survival value can be guessed at. The fouling of the nest might be harmful to the chicks. More to the point perhaps is that prolonged voiding of the faeces over the rim of the nest might betray its presence to a predator. It is true that many birds are careless to say the least where sanitation is concerned, but on the whole this is true of the larger or more predatory species, such as hawks, that can afford to be careless.

How different are conditions in a colony say of nesting herring-gulls, intensively studied by Tinbergen, or of some other bird with young that are nidifugous, abandon the nest that is to say soon after they are hatched. A few hours after emerging from the egg the chicks, warmly wrapped in down and able to stand, begin to beg for food. With herring-gulls, each pair controlling a territory within the colony, the food is regurgitated in a half-digested condition and presented to the chick. But to do this the parent requires a releaser, and the chick provides it by a pecking movement directed not merely vaguely towards the parent, but precisely to its bill, and even more precisely to the red spot near the tip of the yellow bill.

Experiments with dummies show that red is the most effective colour. Spots of other colours evoke less response, a 'bill' devoid of a spot scarcely any at all.

That is one form of close mutual relationship between parents and young. Soon comes another. Within a few days the chicks are scurrying actively about the territory. Consequently they have to be defended from predators, and an auditory releaser comes into play. The instant that a marauder appears the adults utter a specific and recognized alarm-note, to which the whole colony, both adults and young, respond. The adults fly up and a few will attack the predator. But the reaction of the chicks is to crouch and freeze in their tracks, relying on stillness and cryptic coloration. The parents can and do inform the chicks of a state of emergency, but are unable to give any idea of the whereabouts of the marauder. Consequently there is a general crouching and stillness. Tinbergen tells of an amusing incident when he himself, concealed in his hide, was the cause of the alarm, and some of the chicks, warned by the alarm-note, sought safety within the hide. The whole colony had accustomed itself to the hide, accepting it as part of the landscape, but a careless movement on the part of the watcher inside was enough to set off the siren.

These examples of varying releasers, evoking a predetermined response, are of course a matter of instinct, but that does not mean that learning plays no part. In creatures as high in the scale of development as birds there is no doubt that it often plays a considerable part, for instance in allowing them to distinguish between harmful and harmless invaders of their territory. The following very remarkable example illustrates this vividly. Several workers have experimented with cardboard models of birds of various kinds attached to some sort of overhead wire and thus made to 'fly' over, for instance, ducks and geese. The most interesting model was that of a bird with a long outstretched protuberance at one end and a short one at the other. If the model was 'flown' in one direction it had the outline of a bird with a long tail and a short neck, resembled almost any kind of hawk, and caused alarm at once. 'Flown' in

the opposite direction, it became a bird with a long neck and a short tail, perhaps a swan, and no alarm resulted.

Many experiments have been carried out to test the learning ability of birds, and they are extremely interesting. From the point of view of the ecologist, however, they have the serious disadvantage of being concerned with conditions so abnormal as to be quite unknown to birds in their natural habitats. Miss Len Howard's astonishing revelations of the great tit's ability to repeat accurately a varying number of beats tapped out with a pencil is an example. Others show that some birds confronted with food attached to a dangling string will pull the food within reach and hold it in that position by placing a foot on the string. Another makes it clear that a jackdaw can be trained to distinguish between the number of dots on the lids of boxes containing or not containing food. There is this much to be said in favour of these highly artificial tests, that they show clearly the surprising ability to learn, demonstrate the latent reserve of learning ability in birds, which can be brought into play when the occasion arises.

Very little work has been done with mammals in their natural surroundings, and obviously the difficulties are very great, not least among them the fact that so many are nocturnal. This means that the ecologist, convinced that there can be no real substitute for observations made in the field, is inclined perhaps unreasonably to look with disfavour on what we now know about the behaviour of mammals, the result almost entirely of laboratory tests or of experiments on domesticated animals.

With this in mind, however, certain broad conclusions can be arrived at, in the midst of a great deal that is uncertain and contradictory. One thing bound to impress the student is that, while many conclusions conform to what he would expect, there are as many, if not more, of which the same could never be said. It is not surprising for instance to learn that the sexual behaviour of most mammals is innate and inherited. But it seems that this holds good only of the lower mammals who, if reared in isolation from their fellows, nevertheless perform sexual actions at full intensity as soon as the necessary stimulus

is provided. On the other hand a young male chimpanzee, in the presence of a receptive female, fails to achieve union. Another unexpected conclusion is that in a number of instances previous practice seems necessary for certain types of behaviour. Thus female rats, accustomed to build nests in anticipation of giving birth, fail to do so if they have been kept in cages bare of nesting materials, even though material may be available when the time comes. Similarly the hoarding of food not immediately needed will not be done by rats that have been reared in cages destitute of any surplus to hoard. On the subject of hoarding it should serve as a warning against trying to interpret the behaviour of animals in terms of human motives to learn that a hoarding animal will often appear quite unconcerned if the food is only partially hidden, or if it is stolen almost at once.

There is little doubt that many mammals are strongly territorial, and that the territory system gives scope for the exercising of a latent ability to learn. Knowledge of the extent and in particular the boundaries of a territory is often gained by prolonged and thorough exploration. Among dormice, and very probably among many other creatures as well, almost everything else – climbing, concealment, nest-building, postures adopted in response to alarm – seems to be innate. All the same the distinction between innate and learned behaviour is frequently by no means easy to draw. If familiarity with a territory depends on learning, it seems that the marking of its boundaries as a warning to intruders by deposits from scent-glands or with urine, is innate. Perhaps we can say that, if the act of marking the boundaries in this way is innate, the knowledge of where the marking should be done has to be learned.

10

MOVEMENT AND DISPERSAL

O'er bog or steep, through strait, rough, dense, or rare
With head, hands, wings, or feet, pursues his way,
And swims, or sinks, or wades, or creeps, or flies.

JOHN MILTON: *Paradise Lost*, Book II

THE behaviour of animals, almost invariably on land and to a considerable extent in water as well, involves movement of some kind, so much so that this chapter is really an extension of the last. But because movement is so general, and because it includes that widely ranging movement from one habitat to another, which we call migration, it is well worthy of a chapter to itself. Bound up with it is the dispersal of animals, that is to say the extension of their range, causing a change in their distribution. Up to the present my concern has been with animals living in the community which is itself a part of their habitat. That will be true of this chapter also, but I shall have to consider as well certain occasions when, for one reason or another, animals forsake their community and exchange one habitat for another, either temporarily or permanently For a start it will be worth while dealing in greater detail with movement as such.

The power to move is considered, and rightly considered, as an attribute characteristic of animals as distinct from plants; and this after all arises directly from the main feature which distinguishes the one from the other. Plants manufacture their own food, and so apart from the need to extend their range, which they do mainly by seed-dispersal, are not required to move. Animals on the other hand are incapable of making food for themselves, are dependent utterly on plants, and so are required to go in search of their food. But the extent to which movement for this purpose is vital to them depends on the medium in which they live. Water is a dense medium, capable

of sustaining a vast amount of food for animals, consisting in itself of course of living organisms, both plant and animal. But water is not only dense, it is in almost continual movement, with the result that nutriment is carried from place to place. For this reason it is not surprising that a great many animals, both in fresh water and salt, find satisfaction of their needs in a sedentary way of life. Their food can be brought to them. This is a state of affairs impossible to land-dwelling animals, whose medium is the far less dense air. But the sedentary animals of salt water and fresh – some of the protozoa, all the sponges, many coelenterates, some of the worms, echinoderms, and molluscs, and one noteworthy representative of the arthropods – are not to be dismissed in this sweeping manner as creatures content to stand and wait while a beneficent providence wafts food into their open mouths. In other words the statement that they are sedentary needs to be qualified, and this in two distinct ways. In the first place many of them have evolved a way of enhancing to their own advantage the carrying capacity of water. By means of tentacles, feathery plumes, and feelers, they create a movement of their own in the water, a tiny and localized current, conveying more food than would otherwise find its way towards them. The food is then filtered out. There are too entirely passive creatures like sponges lacking this ability. With them it is a matter of flushing water through their bodies, extracting food from it in the process.

The second qualification is more directly concerned with movement, for the truth is that these creatures are sedentary for a phase, the final phase of their life-cycle, only. In the earlier, larval phase they are creatures that move by means of cilia arranged in tufts and girdles on their bodies, the continual lashing of which impels them through the water. It is true that this power to move is very limited and it leaves them almost entirely at the mercy of currents which impart movement far more effectively than any effort of their own. Nevertheless they are animals with the gift of independent movement to a recognizable extent. This is true of the larvae of all the sedentary animals of salt water and fresh. It is true even of the protozoa

whether provided with a single flagellum or whiplash, or with batteries of cilia in girdles and tufts. It is true at certain time, even of those protozoa like *Vorticella* that spend most of their lives fixed at the end of a contractile stalk.

Even this does not exhaust the possibilities, and it is reasonable to include an occasion for movement taking place before the animal has properly come into existence at all. Every animal in whose reproduction sex plays a part is the result of the union of two parental cells, the ovum and the sperm. These indeed are scarcely to be classed as animals, but at least they are the necessary precursors of animals, and of them the sperm has the gift of movement. It is fully capable of propelling itself, and must do so if it is to find and impregnate the ovum, whether that ovum is inside or outside the body of the female.

What all this amounts to then is that all animals without exception are capable of movement at some stage of their existence; and the point to be made clear now is that this power of movement has two quite distinct and fundamentally important functions to perform. The first is to enable the animals to find food for themselves and at the same time, except for those at the upper end of food-chains, to serve as food for others. They become in fact a part of the food-cycle of their community. The other function is to effect their dissemination. With the sedentary creatures the primary compulsion, and the means by which both these functions are performed, is to find some suitable resting-place for their sedentary stage. It is a matter of their lodgment within a habitat that suits them, where they can realize their destinies, find the food they require, and pass on the torch of life by propagating their kind. During their larval stage they are likely to find themselves in an alien habitat, and it is up to them to locate a suitable one. In a great many instances it is nearer the truth to say that the habitat locates them, in the sense that they are carried to it if they are lucky. The vast majority of these ciliated larvae never find a suitable habitat, even if they pass the first stage of all which is that union of ovum and sperm necessary to bring them into existence in

the first place. Uncountable millions of ova, uncountable millions of sperms, perish before they can find partners and unite. Uncountable millions of ciliated larvae also perish at one stage or another, and we refer to this with a superior shake of the head as exemplifying the prodigious wastefulness of nature. But in nature nothing is ever wholly wasted. The astronomical hordes of unfertilized ova, of unfunctioning sperms, of sacrificed ciliated larvae, all go to swell that great reserve of organic substances and of inorganic salts which is never exhausted and is continually drawn upon, so that the cavalcade of life shall keep forever on the move.

So much for those animals that in the final phase of their lives we call the passive ones, to whom movement is no longer necessary. What of the rest, the more highly developed aquatic creatures, very nearly all the arthropods, most of the molluscs, and all the fishes? To them movement is life, whatever their habitat, whatever their stage of development. Movement is essential too for nearly all animals living on land. For these active ones in both elements, because movement is essential, the power to move is more highly developed, giving a greater degree of independence, so that they can defy to a varying extent both currents in water and winds on land. It will be proper to examine the degree and the variety of their movements, to make some attempt at classifying them from this point of view; but I should like to go back for a moment to the passive ones, to two examples of them, so as to point out that the sedentariness of some apparently sedentary creatures is to a large extent illusory.

Consider the acorn barnacle (*Balanus balanoides* – though there are other species and one other genus of this interesting but commonly disregarded creature), which has been referred to previously in connexion with the enormous populations or demes into which it congregates over all our rock-girt shores. My concern now is with the life history of the individual. It is in the first place, not a mollusc as was thought at one time, but a crustacean, a relation of the crab and the lobster. Their prodigious crowding together has nothing to do with making easier

the chance meeting of eggs and sperms, since fertilization strangely enough is internal, brought about by the insertion of a male organ, an inch or more in length, from one individual into another. Acorn barnacles are hermaphrodites, the organs of sex of both kinds being found within each individual. But they do not fertilize themselves. Hence the crowding together is essential if there is to be any fertilization at all. An acorn barnacle isolated from its kind by much more than an inch is condemned to sterility.

The young barnacles then are extruded not as eggs, even fertilized eggs, but as free-swimming larvae with three pairs of legs, a condition in which their crustacean nature becomes clear. Later a more advanced stage is reached, in which they acquire a bean-shaped shell and six pairs of legs. This cypris larva (Plate 10a) does not swim, does not even feed. It has one business in life and one only, to find a resting-place, so that from it the final adult stage may arise. The all-important point is that the cypris larva is not content with a mere hit-or-miss method of finding an anchorage. It uses its legs, of which one pair is set far forward, to explore a rock surface in a way that looks very like careful selection. What appear to matter most are a rough surface and subdued light. Under laboratory conditions, the only ones possible for observing this remarkable 'choosing', it has been watched covering up to half in inch in an hour. Having, as we might not unreasonably say, satisfied itself, it settles down to a sessile existence. The legs become the plumed feelers for raking in food, and it is then the creature of whom it has been said that it stands on its head and kicks food into its mouth. Here then is an animal that uses a random, broadcasting method of dispersal, but one that culminates in a phase that is far from being random. How far this is true of all animals that broadcast their young is a question not yet satisfactorily answered.

The other apparently sessile creature, equally well known, is the common limpet. The seaside visitor who gives the limpet a thought almost certainly considers it very much of a sedentary animal, so much so that it is not easy to dislodge it from its

perch. But I need say no more about this equally nicely adapted creature, for I have described already its pastoral existence, grazing off the algal deposit that coats the rocks. The limpet, in spite of its fixity of tenure when exposed to the air, is an animal habituated to movement, not during the larval stage only but throughout life.

Movements classified

I am concerned here with the whole world of animal life, since as we have seen, movement, whether at one stage or for the whole of their lives, is characteristic and essential. It begins from the time when they are launched into the world, either as larvae or as eggs which presently hatch. This phenomenon, so varied and so universal, can be classified according to the reasons that prompt it, but this is not easily done except into rather loose categories that tend to overlap. That is true of nearly all classifications, and in this instance the attempt is worth making.

MOVEMENTS OF THE HABITAT. First of all it will be as well to dispose of one enormously important class of movement, important because it has gone on continuously throughout the history of life on this planet, and because it is certainly the basic factor in the dispersal of animals and consequently in their geographical distribution at any one time. I have referred to it in the chapter on changing habitats. It is that movement, not of animals as such, but of whole animal communities, inevitably and involuntarily resulting from the movement of their habitat. This is caused in the first place by plant succession, beginning with a bare area and ending with the climax determined by the climate of the part of the world concerned. As we saw, it is this that ultimately gives rise to the great natural regions, consisting of different kinds of forest, different kinds of grassland, different kinds of desert or semi-desert. Then there is that much slower kind, by which the natural regions themselves change, advancing in one place, retreating in another. In both of these,

the animal communities move, are dispersed, because they cannot help it, migrate because their habitats migrate.

Two important points must be added to what has been said previously on this score. First is that on occasions this large-scale, involuntary migration acts in conjunction with warpings and risings of the earth's crust, and with natural selection, to produce very striking results indeed, some of which may be of great importance even today. Consider, for instance, the well-known fact that the continent of Australia and the islands surrounding it are populated, apart from recent introductions, by mammals almost exclusively of one kind, the marsupials, those that is to say that bring forth their young imperfectly developed and housed for a time in a maternal pouch. These are quite distinct from the later, placental mammals, whose young are more or less ready for active existence from the moment of birth. How has this very striking fact come about? To answer we must go back to the time when the early mammals were being evolved from reptiles, some hundred million years ago. Most of these were marsupials, and their stock soon began to branch out into forms suited to various habitats in that adaptive radiation already described. How far this process had gone we can scarcely say, nor can we tell except vaguely where it was going on, but probably in a number of places. For present purposes it is reasonable to assume that one of these was what is now the Asiatic mainland, and that a slow drift of these early marsupials was carrying them eastwards along the present great chain of islands that we call the Indonesian Archipelago and so eventually to the Australia of those days. We cannot of course be certain that the cause of their migration was the involuntary one of the migration of the natural region to which they belonged, but it seems a reasonable supposition. This probably took place during the early part of the Tertiary Era, and a little later, after the movement was complete, Australia became cut off from the other land masses by a sinking of that part of the earth's crust. The all-important result was that the marsupials of that region were isolated in a great stronghold of their own. Their adaptive radiation, however far

it may already have advanced, went on probably at a quickened tempo, into a variety of marsupial forms approximating to, possibly exceeding, the hundred or more species found in Australia at the present time: the grass-eating kangaroos and wallabies, the root-eating wombats, the insect-eating bandicoots, the carnivorous cats and rats, the fruit-eating phalangers. Each group, and each member of the groups, found its niche, its characteristic diet, and became adapted in a number of ways to its mode of living.

In the meantime placental mammals had evolved in other parts of the world and during the greater part of the Tertiary Era underwent their own adaptive radiation, competing as they did so with the marsupials, and competing so successfully that in time they supplanted them altogether, apart from a few in South America. But except for certain bats and probably the dingo they never found their way to Australia because of the continued isolation of that continent. In Australia the marsupials were free to thrive and to evolve in their own way, and so came to dominate it and its encircling islands as they do to this day. A hundred years ago the naturalist Alfred Russel Wallace, jointly responsible with Darwin for the theory of natural selection, traced the frontier dividing Australian from Asiatic mammals, marsupials from placentals. Known as Wallace's Line, it passes between the two small islands of Bali and Lombok, thence through the Strait of Macassar between Borneo and Celebes.

The second point about these slow, compelled migrations of animals with that of their main habitat, is to relate it with their other movements. It is clear that these other voluntary and habitual movements are carried on at the same time, that the large-scale general movement embraces all those made necessary by their daily lives. They are like passengers on a ship, walking the decks, playing games, dining and dancing, when all the while they are being carried steadily in one direction by the revolutions of the ship's propellers.

Naturally this migration of habitats has been of far greater importance with land-dwelling animals than with aquatic ones.

But aquatic creatures cannot be excepted, since rivers change their course, form loops and meanders which are continually being cut off from the main stream, thus first extending the range of such animals, then isolating them. Lakes tend to fill up and to be brought into existence elsewhere by some natural damming up of rivers. As for the sea, the principle holds good

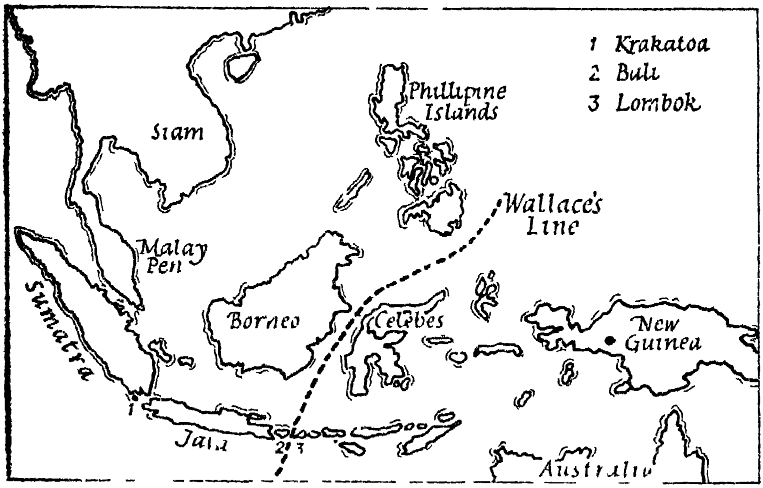

Figure 7. Wallace's Line dividing Asiatic from Australian fauna.

there too, at least so far as marginal, shallower seas are concerned. It seems likely that the great oceanic basins of the world have remained substantially unchanged, though some would deny it, but their margins fluctuate continually. It is unlikely that geologists could point to any part, however circumscribed, of any of the continents that has not been submerged at one time, or more probably over and over again by transgressing seas, drowning plains, and the lower slopes of mountains in one place, laying them bare in another.

As for land animals, to say that this migration has played an important part in their dispersal is certainly an understatement. It is nearer the truth to say that it has been the one major factor.

It is true that many animals do on occasions exchange their habitat for another, sometimes regularly. But it is not too much to make out that these on the whole are abnormal occasions. Animals, as a general rule, stay at home, if only for the reason that home provides the conditions to which they are adapted. It follows that if they move on a large scale it is because their homes are themselves on the move. The process is going on at the present time, and some of it we can see and measure. We hear a good deal nowadays of deserts being on the march, of widespread increasing desiccation in the interior of continents. If the margins of deserts are advancing, as undoubtedly they are in Africa and North America, either from natural or human causes, then the animals characteristic of those deserts cannot fail to advance with them. We learn also of glaciers in retreat in mountainous parts of the world, of the southern limit of the pack-ice in the Arctic Ocean withdrawing northwards. If this is happening, the plants and animals of tundra communities at some distance from the glacier-fronts will slowly advance as the ice retreats. Fishes and other animals demanding rather warmer conditions will similarly follow the recession of the pack-ice.

MOVEMENTS WITHIN THE HABITAT. It is time now to turn to those comparatively small-scale movements of animals, those that we can call for the most part voluntary and incidental to their way of living. For what main reasons are these movements undertaken and what part, if any, do they play in the dispersal of the animals concerned? Apart from sheer enjoyment, as for instance in soaring birds, four main reasons can be rather loosely distinguished, of which three may reasonably be called normal, frequent, undergone by animals to a very large extent as members of their communities, though included within these three are some involving an exchange of one habitat for another, and one which cannot entirely be considered voluntary. They are: firstly drift, applying to an enormous number of very small animals, but also to some larger ones, and caused by currents in water on the one hand, and by winds over both land and sea on the other; secondly movements in search of food and in seeking

safety from predators; thirdly those associated with breeding. The fourth kind of movement, that which is more of an abnormality than the others, is that occasioned by overcrowding. Something must be said of each of these.

1. *Drift.* Since this is caused by agencies of wind or water quite external to the animals themselves, it must be considered as involuntary. The animals, though capable to a limited extent of movement by their own effort, are carried along whether they like it or not. Some, like the unicellular, planktonic plants and animals, may be said to like it to the extent that this is their normal experience. Living in the almost illimitable habitat of the open sea, they drift about, feeding and reproducing within its far-flung boundaries. As we have seen, they play an enormously important part in the ecology of the sea. Apart from these there are the equally countless hordes of larvae who depend on currents for the fulfilment of their life-cycles. Currents perform the necessary service of conveying them to that resting-place for their adult phases, where some will be fixed in one spot, while others move about in quest of food and of mates. Though temporary members of the plankton, they swell its numbers to an incalculable extent.

A third category of these drifters may be said not to like the process in the sense that drifting is no necessity of their normal existence, but befalls them accidentally, sometimes even disastrously. This happens much more frequently in the air than in water for the important reason that the atmosphere can never be regarded as a habitat for living things in the sense that the open sea so abundantly is.

Two examples of this accidental drifting of animals can be given. In 1924, as recorded by Dr Charles Elton, the sledging parties of an expedition to the Arctic came upon great hordes of aphids in the barren snows of Spitsbergen. These insects belonged to the habitat of the spruce forests of Northern Europe, and it was calculated that they had been carried on the wind for a distance of eight hundred miles. Naturally they perished in Spitsbergen almost at once. The same writer tells of dragonflies arriving on the coral islands of Cocos-Keeling. For

a time all was well, and they laid eggs after the manner of their kind in pools of fresh water. But these pools were quite unsuitable and the dragonflies left no descendants on Cocos-Keeling. Clearly in both these instances, if circumstances had been different notable dispersals of aphids and of dragonflies might have resulted. As things were, the aphids landed in an environment that forbade survival, while the dragonflies, though able to survive and even to breed, could not establish themselves as species. Accidents of this kind must be frequent, though it is true that some have happy results, and we know that aphids at least depend normally on air-currents for their dispersal. These two examples are useful because they show that for successful dispersal three conditions must be fulfilled. A species landing in a new habitat must be able to survive even if only to the extent of a few individuals out of a great horde. Having survived, some of these few must find mates, and, having found mates, must succeed in rearing a brood. Only then can there be a chance of the species extending its range.

There is no doubt that air-currents play a big part in the dispersal of some insects, though it is only in recent years that the insect population of the upper air has been fully investigated. This was done by means of nets attached to the cables of barrage-balloons. Results were surprising. It was found that during the summer months a column of air one mile square between heights of 1,000 and 2,000 feet contained a quarter of a million insects, while a similar column below 1,000 feet contained nearly a million. These were mainly aphids, minute flies and equally minute hymenoptera. These and other insects have been caught in traps on aeroplanes up to a height of 14,000 feet.

Apart from the air-currents themselves it seems that temperature is the climatic factor having the greatest influence in populating the air with these hordes of involuntary passengers, and this is what we would expect. When the temperature is high more insects hatch out, and more are likely to be on the wing for the wind to bear aloft. Also at such times hot air-currents are more likely to take them up.

If this transportation by the wind, with its consequence in many instances of dispersal to a considerable distance, is of biological importance to many species, as it seems that it must be, we would expect them to have evolved adaptations to make it easier. This is true of some, though with the great majority their minute size is no doubt adaptation enough. A rather remarkable example is the larva of the gipsy moth (*Porthetria dispar*), introduced from Europe into the United States, where sometimes it becomes a serious pest by defoliating trees. These caterpillars have been caught in traps on aeroplanes up to a height of 2,000 feet in sufficient numbers to show that their dispersal is brought about effectively by the wind. They are covered with long hairs, usually considered an adaptation to make caterpillars unpalatable to birds, but with these gipsy moth larvae it appears that the effect is to make them so buoyant that they can remain airborne for long periods at a stretch. Another adaptation is that used by many species of spider, which during the spiderling stage extrude filaments of silk from their bodies and are dispersed widely by air-currents. It is this that gives us one of the most delightful sights of autumn, the long grasses of a meadow gently heaving with a shimmering carpet of gossamer.

But we need not confine ourselves to insects and spiders, for it is now beginning to be realized that drift dispersal by the winds has played a part of some importance in the distribution of birds. A case in point is Darwin's finches of the Galapagos Islands, cited in the chapter on evolution as an example of adaptive radiation. These birds appear to be descended from an ancestral finch stock invading the islands, which may very well have been blown thither by the wind. A much more recent example occurred in 1937, when fieldfares from north-west Europe successfully colonized Greenland.

While on the subject of birds I cannot resist referring here to the common swift, though this has nothing to do with dispersal. This familiar bird, hurtling with shrill screams over our chimney-pots from May to August, is most beautifully adapted not to be itself carried by the wind, but to take advantage of the

fact that hordes of small insects are so carried and therefore become an important source of food. The swift probably comes nearer than any other creature towards making the air its appropriate habitat. Airborne for the greater part of its life, it feeds entirely on airborne insects, collecting them in close-packed balls in its mouth for its nestlings; gathers airborne materials for its nest; frequently mates on the wing, which is an achievement that can be credited, so far as we know, to no other bird; and so far as non-breeding yearlings are concerned, even spends the whole night on the wing.

2. *Movements connected with food and with predators.* These are the movements incidental to the lives of animals as members of their community, those necessitated by the urgent quest for food, and the equally urgent security, so far as that is possible, from predators. Because they are essentially home movements, they have little bearing, if any, on dispersal. For that reason also they can be dealt with briefly since they have figured prominently already, bound up as they are with food-chains, niches, territories, with competition generally and the restrictions imposed upon it. They figure also in cooperation between members of the same species, that urge towards varying degrees of social integration, involving movement of flocks and herds, as well as those highly organized movements incidental to life in an insect-colony. They have their place also in the behaviour of animals, particularly in that phase of appetitive behaviour, as described in the last chapter, when the animal goes in search of the releaser which brings its reaction specific energy into play.

All that need be added here is that these movements vary enormously according to the mobility of the animal and the extent of its habitat. They vary in this respect all the way from the movements, if any, of a parasite in the gut of its host, and those concerned with its changeover from one host to another, to those prolonged and extensive movements in search of a fresh supply of food that deserve to be called migrations. Intermediate between these extremes, lies for instance the continual activity of small birds endeavouring to satisfy a brood of nestlings. They would range for this purpose over that part of their

habitat which they regard as their territory, and in many instances beyond its limits. Similar movements, but with a far greater range, are those of a pair of gannets in a nesting colony, whose territory is no bigger than the immediate surroundings of the nest, but who glide on their great white wings over many miles of ocean in their quest for fish. Movements amounting to migrations are those of the caribou of the Canadian Arctic, taking place seasonally in search of pasture, northwards towards the coast in the spring, southwards to upland grazing grounds in the autumn.

3. *Movements for breeding purposes.* This brings me to what in many ways are the most interesting, and often the most sensational, of all the movements of animals, those much studied migrations to and from a breeding station. Not all of them are sensational or extensive to a marked degree, including as they do the convergence of birds such as gannets, herring-gulls, terns, to form a nesting colony in the spring, or the congregation of fish such as cod at spawning-grounds in the North Sea. But it is the far ranging migrations of many kinds of bird, of one or two sea mammals and of one very remarkable fish, unnecessarily far-ranging as so many of them seem, and still imperfectly understood, that must engage our attention here.

One point emerges clearly, that these are movements differing from most of those already dealt with, in that they take animals far beyond the limits of one habitat into another and often entirely different one. What lies ultimately behind it all is that a particular habitat becomes unsuitable for a part of the year, whereas another fulfils the requirements then becoming urgent. The result is a migration, becoming of such paramount importance for the species concerned that the immense hazards involved, the pitifully enormous mortality inevitable to the change, are nevertheless worth while. The time spent in the two habitats is often so nearly equal that it is difficult to say which of the two is the normal.

As always, it is satisfying in the midst of so much that remains mysterious to find a general rule governing these migrations; but again as always, there are notable exceptions. The

rule or tendency, which is perhaps a better word, is this: breeding during spring and summer takes place in high latitudes, far from the equator, while winter quarters are in lower latitudes, those more nearly equatorial. This holds good for our summer migrants, coming to us to breed and making the return journey in the autumn to some part of the African continent, in many cases far to the south of the equator. It holds good for our winter migrants, like the fieldfare and the redwing, that breed in northern Scandinavia, travelling southwards to these islands on account of their milder winter. It holds good also for a mammal like the fur-seal which breeds in great colonies in the Pribilov Islands in the Bering Strait, and winters so far as the mature males are concerned in the Gulf of Alaska, a comparatively short distance to the south, while the mature females and young pass the winter 3,000 miles away, off Southern California.

These and many others, astonishing as their journeys are, do what seems to us the reasonable thing, winter in a warm climate, breed in a colder one. But what are we to think of the almost incredible journey of the Arctic tern, which breeds far to the north, at no great distance from the North Pole, during the northern summer, then flies south along the whole length first of the North then of the South Atlantic, to pass the rest of the year on the pack-ice of the Antarctic? Why travel half round the earth, from one polar region to the other, even though this means summer conditions, such as they are, in both? Wilson's petrel reverses this procedure, travelling almost as far, for this bird breeds in the Antarctic and winters in the latitudes of Labrador and western Scotland.

The story of the fresh-water eel, though the adjective is something of a misnomer, has been told frequently since the mystery of its breeding habits was cleared up some fifty years ago, but it is a very wonderful story indeed and perhaps can be told once more. This common fish of our lakes and rivers spends quite a long adult life, up to as much as nineteen years for females and twelve for males, within the continental interior of Europe. At the end of this time a number of changes come

over it. Eyes and nostrils enlarge, the snout becomes more pointed, the general colour changes from yellowish to silvery. Then the urge to travel masters it and it sets out on its journey to the sea, often gliding for short distances overland across the wet grass from the enclosed waters of its home. Reaching the Atlantic, it embarks on the last and far the longest stage of its journey, out into the open sea and westwards, but somewhat south of west, as far as the Sargasso Sea, at least 3,000 miles away. Here the European eels are joined by those from North America. This journey to the breeding grounds takes some six months, and during this period it seems that no food is eaten. Here in the western Atlantic the eels breed, though nothing whatever is known of their breeding habits, or of what then happens to the parents. All we know is that the larvae, still called *Leptocephalus* as though they were of a different species, as was once believed, begin to travel eastwards in a journey which is even more extraordinary than that of the adults. For now the travellers are flat, transparent, leaf-shaped creatures, no more than ten millimetres in length, and yet the journey is as before. In their millions they set out, the North Atlantic Drift aiding them to some extent. By the time they reach the western coasts of Europe they have been three years on the way, and are no longer *Leptocephalus* larvae but elvers, and it is as elvers, some three inches in length, that they enter the mouths of our rivers and make their way to far inland waters, where the cycle begins anew.

These and other astonishing journeys, including those of migrating birds, pose a number of problems as yet very largely unanswered. What is their significance to the species concerned? How have they come about? What biological advantage do they confer, so that natural selection has perpetuated them in spite of the tremendous mortality inevitably taking toll? What is it that gives these creatures the urge to travel at all, let alone to make such prodigious journeys? Above all how do they find their way? Answers are tentative in the extreme, little more than informed guesses. To some of the questions there are no answers at all. As for biological advantage, beyond

realizing that cogent advantage must exist, we are almost completely in the dark. With regard to some of the birds length of daylight seems important. It has been pointed out for instance that the feeding requirements of nestling warblers are so exacting that if breeding took place in equatorial latitudes, the parents simply would not find the time, during the short periods of daylight prevailing there, to satisfy their broods. So they prefer to breed in higher latitudes where, during the summer, day is far longer than night. This presupposes that birds resident round the equator are not faced with that problem. There is good reason on the other hand to suppose that light does indeed play a part of considerable importance with some birds, not because of the proportion of daylight hours to those of darkness, but because of the increasing intensity of light during the spring. It has been proved for example that some birds can be induced to migrate before the normal time by subjecting them to artificial light, and that this has a stimulating effect on the ripening of their sex-organs. This does much to explain the nature of the urge prompting the birds to migrate in the first place, but tells us nothing as to the advantage that migration brings.

Some theories, such as the one just mentioned, can be proved or disproved. Others, because they are bound up with conditions that can never be reproduced, cannot, and as a result never advance beyond the stage of enlightened speculation. Of these there are two that are highly ingenious, convincing up to a point and of special interest because they link up the migration of animals with major events in the history of the earth. They possess in addition the very considerable merit of going some way towards explaining not only how some of these migrations originated, but also how the travellers learn to find their way. One concerns eels, the other the north–south journeys of many birds.

The chief weakness of the theory seeking to explain the otherwise inexplicable journey of the eels is that it presupposes the validity of another theory, that of continental drift. According to this, the continents were at one time clustered together and

have subsequently drifted apart. The Atlantic, if it existed at all, was once no more than a comparatively narrow sea where, we may suppose, European eels had already established a traditional breeding place. Then what is now North America began to drift very slowly westwards, taking with it the breeding place of the eels. The distance between the two continents lengthened over millions of years, so that adult eels migrating westwards on the one hand, and *Leptocephalus* larvae migrating eastwards on the other, were compelled to make longer and longer journeys, of the order in the beginning perhaps of a few score, now of some 3,000 miles. This theory is not so fantastic as it sounds, since the evidence in favour of continental drift is quite impressive, though it cannot be gone into here. As for the eels themselves, it explains how their migrations originated; and their ability to navigate, if their journeys were very slowly extended over millions of years and so became traditional and learned, even possibly hereditary, loses most of its mystery. But it would explain something else as well, and that is their very long larval stage, when growth is extremely slow, paralleled in no other kind of fish and otherwise inexplicable. We might go so far as to conclude that the breeding behaviour of the eel lends support to the theory of continental drift.

This delightful theory, it should be made clear, applies only to the European eel (*Anguilla anguilla*), since no other of the five species of fresh-water eel makes journeys of anything like the same length. The late Professor Leon Bertin however, in his monograph on eels, will have none of it, preferring to explain these astonishing journeys as the result of the successive subsidence from west to east of a lost land-mass, a sort of Atlantis, on the site of the present Sargasso Sea. The European eels, he supposes, breeding in these warm coastal waters and migrating landwards to the fresh-waters needed for their adult phase, were forced to follow this progressive west to east subsidence until it took them very slowly year after year some 3,000 miles, to where the coastline of western Europe now lies. I confess to finding this explanation less convincing than the other, particularly since the theory of continental drift has

recently received notable added support from the study of the magnetism of certain rocks.

The north–south journeys of so many birds can conceivably be related to withdrawal of another kind and one that is fully authenticated, the withdrawal of the ice-sheets, probably the last at the end of the Ice Age. This, as we have seen, meant the slow northward march of a habitat well provided with trees, with insects and other food for birds, and one moreover which extended farther and farther into latitudes with a long summer day, giving abundant opportunity for feeding the importunate nestlings. Is it not possible, is it not indeed highly probable, that creatures as intelligent and as highly mobile as birds, or at any rate some of them, were capable of observing this interesting fact for themselves and of taking advantage of it? These, resident originally all the year round in southerly latitudes, formed the habit of following the ice-sheets year after year as they retreated into a region very favourable for breeding, and having bred there during the spring and summer, made the return journey in the autumn at the onset of wintry conditions. Some would venture further north than others. Some, on the other hand, would remain in their established home throughout the year. The journeys of the migrants were repeated annually, and both the journeys and the ability to navigate would become traditional by slow degrees, learned from their elders in the case of young birds following their parents, hereditary perhaps in time with young birds travelling on their own. The theory of course falls far short of explaining all the migratory journeys of birds; nor does it explain the homing instincts of many birds. But it goes part of the way and explains much, although it can never be proved.

An essential feature of these and of many other migrations that do so much to excite our wonder, is that they are regular, normal and follow a prescribed route. From that it follows that they would seem to play little part in the dispersal of animals. If this should happen it would be in the course of these seasonal journeys, incidental to them, or perhaps accidental would be a more accurate term. Violent cross-winds, for example, could

and undoubtedly have blown birds far out of their course, and this might result in dispersal, but such an event would be rare since, as we have seen, for birds to survive such treatment is one thing, to become established as a result quite another.

The supreme mystery connected with these journeys is the method of navigation used by the travellers. A great deal of ingenuity has been expended in the quest for an explanation. Many not unreasonable theories have been propounded, not to mention a number of wild guesses. Some progress has been achieved, but not much. Rejecting the theory of continental drift as too far-fetched, we have not the remotest idea as to how adult eels find their way from the river-mouths of western Europe to their breeding ground in the Sargasso Sea, still less how the *Leptocephalus* larvae find theirs on the return journey, except in so far as the North Atlantic Drift carries them passively, which is far from being a complete explanation. One suggestion is that it is a matter of detecting minute differences of salinity or of temperature.

Similar ignorance has to be confessed with regard to another and very remarkable migration of this normal and regular kind not yet mentioned, that of many species of butterfly. These for the most part conform to the general rule of polewards in the spring, equatorwards in the autumn. Since butterflies are such short-lived creatures it is not surprising to find that in most cases breeding takes place at the end of both journeys. The European painted lady, for instance, breeds in North Africa during the winter, crosses the Mediterranean, flies north, and after a while begins to breed again, on occasions reaching as far north as Scotland. It is the butterflies hatching from the eggs laid near the northern end of the journey that set out on the return flight. On the other hand it is now known that individuals of the American monarch butterfly are capable of making similar journeys in both directions. A very striking feature of butterfly migrations is the astonishing steadfastness of direction kept up. There are records, for instance, of their flying through a window on one side of a house, and out through another on the

opposite side; another of a swarm that flew up one wall of a house, across the roof, and down the other side. In America it has been noticed that monarch butterflies on migration rest in festooning swarms on the same tree year after year. One most mysterious incident is on record in which a swarm of the same species made a right-angled turn in the middle of a long inlet leading south from Lake Ontario, then corrected the deviation with another right-angled turn, and flew on over their original course, all this for no apparent reason at all. How do migrating butterflies find their way? We have no idea. It can be added that, in the opinion of a leading authority, wind direction is of no significance.

How do salmon find their way from the sea to the mouths of the rivers in which they were hatched? This is what happens in the normal course of events, for this splendid fish adopts a breeding-procedure opposite to that of the eel, making its way from the sea up rivers to spawn far inland in the headwaters, then returning to the sea. How do they recognize their home waters, particularly since three or four years normally elapse between the first arrival of a young fish in the sea and its journey inland to spawn? We have no idea. It appears though that the knowledge is learned and not hereditary, though that tells us nothing as to the nature of the knowledge. The conclusion that it is a matter of learning, and therefore of memory, was strongly suggested by an interesting experiment carried out on the Pacific Coast of North America. Eggs laid in one river were moved to another. The salmon that hatched from them were allowed to stay there until they were several months old, and were then marked and released. Four to five years later they were recaptured in every instance in the river in which they had spent those first formative months, and not the one in which the eggs from which they were hatched had been laid.

But it is birds that have attracted most attention, and it is among them that the beginnings of progress towards a solution have been made. The mystery has to some very slight extent been dissipated, even the mystery of how young birds, unaccompanied by their parents, find their way over long distances

which they have never traversed before. But this partial modification of mystery leaves wonder enhanced rather than impaired. It must be made clear, even at the cost of repetition, that the theory already described relating the journeys of birds to recession of the ice-sheets can go only part of the way towards solving the problem. Route-finding could in this way have become traditional, in which event young birds would follow their elders who have covered the ground at least once before. But among many birds this does not happen, and in any case it seems likely that the art would have to be hereditary if the facts are to be explained. But this conclusion takes us very little further, since it fails to explain by what means this skill is exercised. Farther than this, the theory about the ice-sheets has no value at all when applied to the unbelievable journeys of the Arctic tern and Wilson's petrel, and even less to that of the solitary Manx shearwater set free in Boston, Massachusetts, to fly unerringly across the Atlantic to its nesting-hole on the island of Skokholm off the coast of Pembrokeshire.

One theory of navigation after another has had to be abandoned – recognition of landmarks, response to the earth's magnetic field, response to obscure forces connected with the rotation of the earth. Recent investigations tend towards the conclusion, and that is about as strongly as we can put it, that a bird becomes aware of its position with reference to that of its home in essentially the same way as human navigators do by means of quite complicated calculations. Birds use, it is believed, the principle of sun-navigation, astonishing as this may seem, aware whether they are to the north or south of their home by realizing the difference in the height of the sun when at the zenith, as between their new position and their home. They need also to know whether they are to the east or to the west of home, and this is made possible because they possess some quite obscurely understood internal timing mechanism which they use in essentially the same way as the navigator of a ship who has a chronometer keeping Greenwich time.

4. *Migration caused by overcrowding*. That leaves the fourth and last type of movement, that brought about by the fact that

conditions in the normal habitat have become intolerable because of an excessive increase in numbers. The result is an overmastering urge to get on the move, a condition in some instances bordering on hysteria, in which what appears to be a blindly-directed emigration takes place, leading to a very heavy mortality among the migrants. It will occur to the reader to connect these catastrophic increases in numbers with those rhythmic fluctuations discussed earlier, and migration will then appear as a sort of safety-valve by which surplus population can be got rid of. This is what it appears to be, though not all rhythmically increasing species relieve the pressure of numbers in this way. Where this does happen, it must have some advantage to the species, in spite of the great numbers of the migrants that perish on every occasion. We can only suppose that if they stayed where they were an even larger number would die. Mass emigration does at least give a few of these creatures the chance of finding a new home, and it appears to be true that dispersal to a limited extent has been known to result.

By far the best known example of these mass emigrations is that of the Norwegian lemming, a small guinea-pig-like creature living in the mountains of Southern Norway, as well as farther north in a similar habitat at sea-level. Their sensational emigrations take place at about four-year intervals, and the first account of one of them was published in the sixteenth century, when it was believed that they had fallen from the sky. When the urge takes them they move in hordes from the mountains towards lower levels, wrought up to an astonishing pitch of excitement, pugnacious to an extent unknown to their normal existence. They frequently swim rivers and thousands are eventually drowned in the sea. There is one account of a ship steaming for a quarter of an hour through a great flotilla of swimming lemmings.

There are many other examples of mass emigrations, of periodic irruptions, into fresh habitats. Some birds are affected, for example Pallas's sand-grouse, a bird of the dry steppes of eastern Europe and central Asia. The crossbill and the waxwing are two more, and from among the migrating flocks of all

three of these, stragglers have been known to reach the British Isles, but no real dispersal comes about. Pallas's sand-grouse and waxwings remain as rare stragglers so far as the list of British birds is concerned, while if the status of the crossbill is somewhat higher than this, no permanent increase in their numbers takes place. Among insects one example is only too well known and of immense economic importance, that of the locust.

The ultimate cause of overcrowding in these and other instances is of course the natural fecundity of the animals concerned, which for some reason has not been checked by normal methods. As soon as a certain pitch is reached, they either stay where they are and die off in vast numbers, or relieve the situation, at least so far as those that stay behind are concerned, by mass emigration. What we need to know is the precise reason that makes the situation no longer tolerable, and that is what we do not know with any exactness. One thing seems certain, that there is no one reason to explain all these periodic movements. In some cases, as with a bird like the crossbill, it seems to be food shortage pure and simple, since these birds have a specialized diet. They live on the seeds of conifers, of which the crop varies considerably from year to year. With lemmings and other rodents it is more likely to be a shock disease caused by the pressure of individuals upon one another. Competition not only for food, but also for cover and perhaps territories, is enormously stimulated. All this leads to a steadily mounting stress through the whole population. This appears to affect certain glands into a condition of morbid activity with pathological consequences in the blood-stream, of which one is an abnormally low sugar-content. It is reasonable to suppose that it is this which causes the hysterical excitement and unwonted pugnacity among migrating lemmings. Shock disease of this kind has been noticed also among snowshoe hares in the Canadian tundra.

I bring this chapter to an end with a summarized account of a theory which may well go a long way towards providing an answer to the problems referred to in the last few paragraphs.

Its author is the Swedish ornithologist Dr Gunnar Svardson, and it was set out in detail in *British Birds*, August 1957. The subject of the paper is the so-called invasion-type of migration displayed by several kinds of bird inhabiting the great belt of mainly coniferous forest that stretches from Norway and Sweden across Finland, northern Russia and Siberia, clear to the Pacific, though Dr Svardson is concerned only with its western, Scandinavian end. I have referred briefly to these invasions already when dealing with the irruptions of crossbills and waxwings into the British Isles, and it is important to distinguish between these periodic and apparently irregular movements, and those regular, seasonal, twice-yearly journeys to and from a distant breeding-ground which we usually think of under the heading of migration.

The reason for these periodic invasions is shortage of food, which for these and other birds, as well as for some small mammals, consists to a very considerable extent of spruce seeds, produced in prodigious quantities over this great natural region. The birds, depending to an extent varying with the species on the supply of these seeds, are forced to migrate when a shortage occurs in one particular part of the forest belt, and to keep moving until they come upon a sufficiently rich supply in some other part. The result is a very noticeable increase in the numbers of one or more kinds of bird, an invasion from the point of view of an observer in one of these periodically favoured regions.

The first important point brought out by Dr Svardson is that the Norway Spruce of the Scandinavian forest, particularly that of southern Sweden, shows a marked periodicity in its crop of cones, a peak with a heavy crop appearing every third or fourth year. The primary cause of this rhythmic fruiting is believed to be a high temperature during the early summer, as a result of which buds bring forth flowers rather than leaf-shoots. The flower-buds develop into cones throughout the late summer and autumn, so that by the onset of winter a rich supply of food is available to the birds just when they need it most. Following upon one of these peak cone-years, the trees need up-

to three years of normal or sub-normal fruiting, as though the effort had tired them and they need an interlude for recuperation. Evidence is provided for concluding that this rhythm of seed production applies not only to spruce-trees, but also to birch, oak, and beech; further that as regards these four, in southern Sweden in particular, the peaks tend to occur in the same year. Pine-trees on the other hand are out of step with the rest because their cones take two years to mature. Yet again it is highly probable, though not yet fully authenticated, that similar rhythmical fruiting applies to shrubs such as whortleberry and crowberry.

The second major factor is that birds such as crossbills, redpolls, and siskins depend to a very large extent on spruce seeds, both for themselves as adults and when they are feeding their young. Nuthatches, marsh-tits, and greater spotted woodpeckers feed at least partly on spruce seeds, and bramblings almost entirely on beechmast. There are many others as well. Game birds, such as black grouse, willow grouse, and ptarmigan feed on the berries of low-growing shrubs; red squirrels on spruce seeds, and small ground-living rodents also on spruce seeds after they have fallen to the ground. It seems therefore that there can be few kinds of bird or of small mammal, living both in the forest and in the mountains above, where willow and birch are the characteristic trees whose lives are not vitally influenced by this rhythmic variation in food supply. Nor must the predators on these seed-eaters be forgotten, taking their place in two important food-chains, one operating by day, the other by night, in the manner I have already described. Spruce seeds are the food of red squirrels, while red squirrels are the food of buzzards, goshawks, and particularly pine-martens. Spruce seeds once more are the food of small rodents, while the same rodents go far to keep alive at least three different kinds of owl.

Here then is a striking forest phenomenon to which nearly all the inhabitants must in some way adapt themselves. It seems that there are in the main two distinct adaptations. The first is these invasion migrations, abandoning a region of

scarcity for one in which plenty for the time being prevails, and it applies to some forty species of bird, which in this way have adapted themselves to the fluctuating fruit production of the trees. But, as so often happens, adaptation is mutual, and it is reasonable to make out that the trees have adapted themselves to their despoilers, to this host of voracious seed-eaters which, if not discouraged periodically by lean years between those of plenty, might go far towards bringing about the extinction of the trees. These invasion migrations over the vast extent of the northern coniferous forest, mainly it is to be supposed in easterly or westerly directions, are practicable only for winged or otherwise fairly mobile creatures. They may perhaps be the explanation of the famous mass-migration of the Norwegian lemming. The other adaptation applies to the small ground-dwelling rodents, mice of more than one kind, by comparison handicapped. No mass migrations for them. Their response is simple and catastrophic. They just die off in enormous numbers during the worst years, hugely multiplying to a corresponding extent in times of plenty. It is the first of these adaptations that Dr Svardson is concerned with in this paper; but it seems likely that his theory can embrace also those otherwise unaccountable population cycles with a four-year rhythm to which so many small northern mammals are subject. These have been mentioned under the heading of migration brought about proximately by overcrowding.

To sum up it should now be clear that the great merit of this highly interesting theory is that it links into a single intricate ecological complex three major phenomena hitherto considered separately. These are in the first place the rhythmical fruiting of many, if not most, perennial plants in the zone of the northern coniferous forest; secondly, the population cycles of many small mammals in the same zone; thirdly, the invasion type of migration displayed by some forty species of its birds. It would hardly be possible to find a better example of the unity of the natural world, of the way in which all forms of life, both plant and animal, are bound to one another by intimate and complex ties.

That is one reflection to which this theory gives rise, but there is another hardly less important. This concerns what we are so inclined to call the prodigious wastefulness of nature. I have written about this already and make no apology for referring to it once more. We think on the one hand of the astronomical production in the sea of ova, sperms, fertilized eggs, and larvae, and are sometimes appalled by the thought that an infinitesimal proportion is ever fertilized in the case of ova, or ever grows to maturity where larvae are concerned. We think also, more directly in this instance, of the corresponding millions of spruce seeds, of the seeds of other trees, and shrubs, of the spores of ferns and of fungi that the great northern forests bring forth year after year. That too seems to be waste on an intimidating scale. But the theory I have outlined makes clear that the bringing forth of all these hosts of embryonic living entities serves not one purpose but two. The primary purpose is to ensure the propagation of the species they represent, as is so abundantly testified by the persistence of living things over countless generations, for hundreds of millions of years. It is achieved by the liberation of an enormous surplus, a surplus that perishes beyond question, but in perishing provides an incalculable reserve of nourishment so that other organisms may live.

11

COLOUR AND PATTERN

Glory be to God for dappled things –
For skies of couple-colour as a brinded cow;
For rose-moles all in stipple upon trout that swim;
Fresh fire-coal chestnut-falls; finches' wings;
Landscape plotted and pieced – fold, fallow, and plough.

GERARD MANLEY HOPKINS, 'Pied Beauty'

ONE more major example of the dependence of animals on their habitat remains. This is an ecological principle of considerable importance, an aspect of animal behaviour, using that phrase in its widest sense. It links up also with the subject of movement, but inversely, since here it is absence of movement that counts. As I hope we have abundantly seen, animals grouping themselves into communities consisting of various species, are themselves a part of their habitat which must be thought of in relation to them, this relationship being of so intimate a nature that we can scarcely have the one without the other. But it is reasonable to think of the habitat in another way, as the background, constantly and slowly changing, to the lives of its animal inhabitants. It is the dependence of animals on this background of theirs that I am concerned with now.

Travellers in the equatorial forest have frequently commented on the silence and the lack of movement, during the daytime at any rate, among the great trees and the festooning lianas. They find it difficult to believe, except at rather rare intervals, that the forest really does teem with animal life. The same is true of the coniferous forests of the northern hemisphere. You may walk all day along some logging trail without becoming aware of the presence of animals, except for the occasional note of a bird or the hum of insects. The larger animals avoid drawing attention to themselves so successfully that you are much

inclined to doubt their existence. In the open country of grassland and desert things are rather different because of the wide vistas. In the African savanna we may still see many of the most superb living creatures in the world wandering in herds. But they, and still more the few solitary ones, do not stand out against their background. The watcher has to use his eyes to some purpose. Much the same is true even of our trimmed and parcelled countryside here at home.

Much of this is accounted for, during the daytime when eyesight comes into its own, by the fact that most of the smaller creatures have hidden themselves away below ground, under stones, or in the heart of thick cover. They are adepts at concealment in all sorts of ways. But this is far from explaining all. The rest is this remaining form of dependence on habitat, the fact that most animals have evolved a scheme of colour and pattern which imparts concealment even when nothing intervenes between them and the eye of the beholder. We call it protective resemblance or camouflage, and it is a principle so varied and so widespread, on occasions involving minute detail, that it deserves to be thought of as an important aspect of ecology in its own right. As such it has received a great deal of attention. Books were written about it and conclusions come to many years before ecology was thought of, when the relationship between animals and their environment, except in this one respect, was for the most part ignored. For this there was good reason. It is now over a hundred years since the publication of Darwin's *The Origin of Species* set naturalists agog with excitement at the thought of evolution, and encouraged them to look everywhere for evidence of the operation of natural selection. Protective resemblance was one of the more noticeable forms taken by this evidence, and so it was inevitable that much should be made of it.

We realize now that too much attention was given to it, but the validity of the principle remains unshaken. The attitude of many of the earlier naturalists was altogether too subjective, since clearly the whole thing rests on the assumption that if predators are deceived by the resemblance of prey to back-

ground, those predators must see colour and pattern as we see them. We cannot borrow the eyes of hunting animals and so prove whether or not they are taken in. The higher animals probably have vision akin to our own, but certainty can be arrived at only by experiment. In a great number of instances this has been done, but that is no reason for applying the principle universally. There are for instance many animals which use scent and hearing rather than sight when they hunt. These are the night-hunters, most carnivorous mammals and some birds. Against them protective resemblance seems of doubtful value. I return to this point at the end of the present chapter. In addition to this there are some animals that either always, or at some period during their lives, flaunt themselves as outstanding exceptions to any general rule of camouflage. They seem to go out of their way to make themselves as conspicuous as possible. The earlier investigators did not fail to take them, or some of them, into account. They were made out to be exceptions that helped to prove the rule, and many of the explanations put forward then have stood the test of time. They will be considered later in this chapter. But we know much more today about this occasional flaunting of fine feathers; know for instance, as I hope has become clear, that much of it has to do with courtship, with rivalry between males of the same species, and with those sensory releasers calling instinctive actions into play

But for all this the evidence in favour of protective coloration is far too impressive, both in a general and in a particular sense, to be ignored. It is in fact impressive enough, especially where resemblance has a detailed faithfulness, to be used as a cogent argument in favour of the efficiency of natural selection. Countless examples of detailed resemblance to background make no sense in any other context. Some of the evidence can now be reviewed, and a distinction can be made between camouflage of a general and of a special kind, though it is not easy to separate the two on every occasion.

General camouflage

By this is meant resemblance not to a circumscribed part of the background, but to the background generally. It applies therefore to the larger, mobile animals that range over a habitat of wide extent. This is far from meaning that mobility confers concealment. On the contrary it is of the first importance to realize that movement, camouflage or no camouflage, means betrayal. Protective resemblance and stillness go hand in hand. What is meant is that an animal camouflaged in this general sense can depend on remaining concealed against a background more or less uniform and stretching over a wide area, provided that when concealment is called for it keeps still. One of the commoner forms of this general camouflage is that known as counter-shading, practised widely among the larger animals both on land and in the sea. The comparatively few furry or hairy animals of a uniform tone all over are mostly nocturnal. In the rest the tendency is for the upper parts to be relatively dark, the lower pale, while the flanks merge in this respect from above downwards. The result is to produce an illusion of uniformity, so that the creature blends with its background. The effect counteracts that produced by light from above, since this, in the absence of counter-shading, would make the animal conspicuous, its underside appearing darker than its back.

This form of general camouflage is found commonly in creatures of an open grassland environment, and may well be valuable in the half-light of dusk and dawn. In the sea the same arrangement becomes doubly useful, for the sea is a three-dimensional world, so that many fish need concealment when seen both from above and from below. Counter-shading gives them this concealment, the dark upper parts causing them to merge into the sombre background of the sea-floor, while the pale belly does the same with respect to the lighter upper levels. Exceptions to rules are always interesting and frequently disconcerting, but there is one kind which can always be welcomed with enthusiasm and that is the kind of exception which goes

far towards proving a rule. Counter-shading gives us at least one notable example. The common water boatman (*Notonecta*) of our ponds and still waters is coloured contrary to the counter-shading rule, pale brown above, dark almost black on the under-surface. The reason for this bold nonconformity is simple. The creature habitually swims on its back.

Another type of camouflage is caused by stripes and blotches which help to deceive the eye by breaking up the general outline of the body, a device resorted to on a large scale by nations in wartime and applied to tents, factories, and ships This is known as disruptive patterning, and becomes important for instance for zebras grazing or slowly on the move at dusk or dawn. It does the same for deer, whose beautifully spotted or dappled coats provide most efficient concealment in dense forest, where sunlight penetrates the canopy of foliage in flecks and beams of radiance. A third device, perhaps the most general of all, is that given by colour harmony Desert animals, with some notable exceptions, tend to be desert-coloured Many of the fur-bearing animals of the Arctic tundra assume a winter garment of white. Among the most gaudily coloured creatures in the world are the fishes of coral reefs and they need to be, since they move perpetually against a background glorious with colour, where sobriety of hue would make them glaringly conspicuous Finally with most of the larger animals the thing that tends to betray their presence is their shadow, and this can be counteracted to a great extent if they take up a crouching attitude, close-pressed to the ground.

These are the more important of the general devices that natural selection has brought into prominence in the course of evolution, and they serve the interests of both prey and predator. Camouflage it is permissible, if conjectural, to suppose was first used to protect otherwise helpless creatures from being devoured. But from the point of view of the species it would not do for concealment to become complete, since as we have seen the predator has its place in the scheme of things even from the point of view of the prey So the leopard learned the usefulness of a spotted hide as well as the antelope on which he preys,

and that other great cat, the Asiatic tiger, acquired his stripes which served him well during his stealthy approach against a background of tall grass similarly patterned with stripes of sunlight and shadow. On the whole though it must be true that camouflage benefits prey rather than predators, most of whom, though not all, are required to move.

Specialized camouflage

Perhaps it is the innumerable examples of specialized camouflage that are the more interesting, so numerous and sometimes so exquisitely exact that they, more than the general devices, give us all the evidence we need for accepting the principle of protective coloration. This is the concern on the whole of the smaller animals, those that have little need for movement, whose lives at any one of their stages are circumscribed within the limits of a single tree, even of a single leaf. It is frequently of immense importance for many animals that do not move at all. Camouflage of this kind is found in all latitudes and in every kind of habitat, practised by citizens of almost all the provinces of the animal kingdom.

ON LAND. Among birds we find the widest difference between the coloration of the sexes, or none at all, but where the two are sharply marked off from one another it is usual for the cock to wear fine feathers, while the hen is soberly clad. The splendour of the cocks has been favoured by natural selection for reasons sufficiently important for the advantage of concealment to be overborne by considerations of courtship, rivalry between males, the maintenance of territories, and the giving out of releasers determining behaviour. Among many birds that nest on the ground concealment may be what counts most where the hens are concerned, since they are particularly vulnerable to predators while brooding the eggs. So we find cryptic coloration among hen-pheasants and among ducks as opposed to drakes.

But it is to insects that we must go to find masterpieces of the

art. Very many butterflies, for instance, are gaudy in the extreme, but usually it is the upper surfaces of the wings that are glorious with colour, while the lower have a mottled sobriety. It is the common, though not invariable, practice among butterflies to raise and clasp their wings together over their backs when they alight, with the result that the sober underside is exposed to view and often blends with the background. The familiar red admiral and the small tortoiseshell are examples. By far the most remarkable instance of this device is the Indian leaf butterfly, the upper surface of whose wings is enriched with purple and orange. But the wing as a whole is shaped like a leaf and the underside is coloured a dead brown Resemblance is far from ending there. Down the centre is a dark line reproducing the mid-rib, while the lower wing ends in a projection corresponding to the stalk More remarkable still, the lower surface bears discoloured blotches indistinguishable from those caused in a leaf by decay

Moths, on the other hand, when alighting usually lower their wings parallel to the body, the upper ones covering the lower. Corresponding to this habit is the fact that in many species the upper wing is drably marked, while the lower has either the whole surface or a single conspicuous 'eye' of some bright colour (Plates 11a and b) Moths frequently rest during the daytime on lichen-covered tree-trunks, and when thus resting are often almost impossible to detect against that background (Plate 12a)

Protective resemblance is by no means confined to the adult stage (Plate 12d) There are, for example, caterpillars which move by a looping action, but have formed the habit of gripping a stem with claspers at the rear end of their bodies and of holding themselves erect at an angle in such a way that in colour, attitude, and markings they are scarcely to be distinguished from twigs. This frozen stance may be kept up for hours at a time, since feeding is done at night. The caterpillar of the waved umber is a good example, so is that of the peppered moth, which provides also such a striking example of industrial melanism (see page 182).

It is by no means unknown for the same insect to camouflage itself in a different way during different stages of its metamorphosis, and there is at least one example of a British insect that adjusts itself to its background in two different ways during its larval stage. To take the second of these first, the larvae of the large emerald moth hatch in late summer and hibernate on the bare twigs of birch trees. At this stage they are reddish brown with a few green markings, harmonizing admirably with brown twigs. In the spring when they rouse themselves, the green markings steadily become more pronounced until green is the dominant tint and harmony is once more achieved, this time with the background of fresh young leaves. As an example of an insect using two entirely different devices at different stages of its metamorphosis, a small beetle may be cited. This is a weevil of the genus *Cionus* found commonly on figwort growing along the banks of rivers. The adult is little more than a quarter of an inch in width, and like all weevils has a long snout. When disturbed it tucks its snout under itself and drops to the ground, or to a leaf lower down on the plant. Here it remains motionless and resembles quite closely the dropping of some small bird. During the larval stage *Cionus* seems to disdain protective resemblance, it is impossible to suggest why, but makes up for this by resorting to it again during the pupal stage. This is undergone within a thimble-shaped, papery cocoon attached near the summit of the figwort plant, where its resemblance to the seed-capsules is quite striking.

IN THE SEA. In the sea opportunities for cryptic coloration are as numerous as on land. Prawns in a rock-pool are sand-coloured in so far as they are coloured at all, and in addition to that are semi-transparent, so that we seldom catch sight of them until they whisk out of sight into the cover of a tuft of weed. A beautiful anemone with a very truncated stalk, known as the dahlia, has thick fleshy tentacles and has formed the habit of disguising itself with grains of sand until it becomes almost a part of its background. As such it can fulfil the more surely its function as a deadly predator. The sea-hare (*Aplysia*) is a

mollusc with a reduced internal shell, little more than a vestige, and wears on its back sail-like outgrowths with a close resemblance to fronds of seaweed. But this is no more than a beginning, for *Aplysia* is a master of the art of camouflage, able to adapt itself to more than one kind of background. It could be cited also as an example of a creature that migrates seasonally for breeding purposes. Beginning life in offshore waters, it comes inshore to spawn, and in the course of this journey, when traversing patches of weed differing in their prevailing colour, it changes its own colour to correspond.

But this is to describe the process too simply Closer examination of the responsiveness of *Aplysia* to colour brings to light a most interesting fact. It appears that the change in colour from one weed-patch to the next is comparatively slight, beginning when the sea-hares are at an early stage of development with rosy red and against weed of the same colour, then graduating shorewards through tints progressively darker to the olive-brown of the wracks that flourish in the zone near the limit of low spring tides. Young sea-hares have been reared under laboratory conditions, and it was then found that even when kept amongst weed all of one colour, they still went through the colour-changes appropriate to their inshore migration. This seems to mean that the young sea-hare, having first undergone a slight change of colour, moves inshore in search of weed of a colour matching its own. In other words the migration of these creatures is deeply influenced, if not brought about, by the colour of its food.

An even more advanced practitioner of the art of camouflage is the spider-crab (*Macropodia rostratus*), for this remarkable crustacean brings into play what looks uncannily like intelligence. It is a spindle-legged, exceedingly angular creature and its carapace is covered with hooked projections which it uses to deck itself protectively with wisps of seaweed. In doing so it shows quite startling discrimination, for experiments have proved that a spider-crab already festooned say with reddish weed, if moved to a background of green weed, will set to work

removing the red weed and donning the green. Deprived of weed of any sort, but supplied with sand-grains and small pebbles, it will do what it can to disguise itself with these. This of course is not really intelligence, and it is doubtful if it can be classed even as learned behaviour. The action must be innate, instinctive, carried out presumably in response to a visual stimulus given out by the weed, and less certainly, where all is cloaked in uncertainty, by the shape and hardness of sand-grains.

The Sargasso Sea, famous as the breeding-place of the European and North American eel, is also a noted school of camouflage. The sargassum weed that floats there has deeply notched fronds and branched stems, bearing fruiting-bodies; while the fish, crustaceans, and worms that pass their lives there, it is perhaps not surprising to learn, are correspondingly flounced, frilled, and notched. Apart from this they are spotted here and there as though encrusted with marine growths like the weed, and wear the same yellow-brown livery of their general background. So successful are they in this intimate and detailed correspondence that it is necessary to shake them out of a tuft of weed before their presence can become known. The sargassum fish (*Pterophryne*), for instance, not only has deeply notched fins but a number of frilled protuberances and weedy filaments of various sizes all over its body, all entirely functionless except as additional camouflage. As well as this its general ochreous 'sargassum' coloration is broken up into blotches and circles, all adding to the same effect.

Yet another example of camouflage among marine animals brings out a special refinement of the art, since it is a case of disguising not the whole body, but one vital part. In Pacific coral reefs there lives a fish called the four-eye, of the genus *Chaetodon*. It possesses of course only two of these organs, but they are camouflaged by a dark vertical stripe passing above and below. But that is not enough. The attention of an enemy must also be distracted from these vital organs, so the other two 'eyes' are false, mere spots conspicuously black and white and placed near the base of the tail. The illusion is enhanced by the fact

that the fish normally swims slowly tail first, but when alarmed darts to cover head first.

THE SUPREME PRACTITIONER. The most skilled refinement in the art of camouflage appears when resemblance, from being merely passive, becomes active, when in other words the animal has the power of changing its colour of its own volition, as the occasion demands. We have seen something of this supreme achievement already and in two different ways, as shown by *Aplysia* and the spider-crab, *Macropodia*, and there are many others. The land-dwelling chameleon has earned a fame that has become proverbial where this is concerned, but there is a creature of the sea that has developed the art of self-induced colour-change to such a pitch that the chameleon figures by comparison as a novice. This is the cuttlefish (*Sepia officinalis*), a member of the order of molluscs (cephalopods) to which the octopus and the squid also belong. The following account is taken from Dr A. C. Hardy's *The Open Sea*. A word or two first as to the mechanism employed. *Sepia* possesses all over its body tiny cells of pigment arranged in layers one below the other, each layer corresponding to a different colour, the outer one yellow, the middle orange-red, and the third dark brown or almost black. Each cell is like a minute bag containing its appropriate colour, and each is controlled by strands of muscle radiating outwards. By means of these muscles the bags of colour can be contracted to pin-points or expanded to an appreciable patch, and the creature can control the expansion and contraction of the bags either of one colour-layer only or of two or more in conjunction. In this way it becomes on the one hand uniformly yellow, red, or almost black; while on the other it achieves subtle combinations of two or of all three, so that alternating waves of colour pulse and waver over the whole surface of its body, whether uniformly spread or as patterns of bars and stripes. By contracting all the cells in these three layers it becomes pure white, for then yet another layer, this time of white rigid cells on a lower level than the other layers, comes into play.

What does all this mean? It means that *Sepia* is not only a master at adapting itself to backgrounds of various colours, but that it practises as well several distinct variations of camouflage, including those I have already described. Thus a pattern of stripes radiating out from a wide bar of dark brown is a good example of camouflage of the disruptive kind, tending to break up the outline of the body. Again because the general colour-scheme at all stages is one of dark tones above and lighter ones below, it exemplifies counter-shading as well. Response to the colour of various backgrounds is extremely quick, for the expansion of the cells has been timed, and full expansion from the pin-point stage takes considerably less than a second. As for variety of response, experiments in an aquarium have brought out an extraordinary degree of skill. A cuttlefish in a dark aquarium is of course correspondingly dark, but place a tile of white porcelain beside it and it will reproduce the outline of the tile as a white rectangle in the middle of its back. When the creature is disturbed by touching it, or by some violent agitation in its field of vision, it responds with a whole series of changes. Spots and longitudinal stripes appear, together with colour-changes so quick as to be bewildering. All this time the creature is darting furiously from place to place. If the teasing continues, it responds with its last resource, that of the smoke-screen, and it shoots out a cloud of ink, behind which it takes refuge. When on the other hand *Sepia* is sulky and disinclined to move, a change appears not of colour only, but of shape as well. From being oval it swells itself out to a circular outline, increasing also in thickness. At the same time the eyes dilate to glaring protuberances. Black spots appear on a body otherwise white, or a black rim encircles the white body. This of course is not camouflage, but its opposite, the assumption of a conspicuous appearance calculated to inspire awe, if not terror.

It must be made clear that these changes of colour have at times a purpose other than escape from predators, or to operate with more deadly effect as a predator itself on the crabs that are its chief food. In the mating season a zebra-like pattern of

alternating white and purple bars becomes its nuptial livery. This acts as a releaser, inducing belligerency in other males and a tranquil submissiveness in females willing to copulate. As if all this were not enough, it has become clear from recent experiments that *Sepia* has a well-developed capacity to learn from experience. All in all *Sepia officinalis* is a highly remarkable creature: there can be very few others capable of being used to demonstrate almost all the principles of adaptive coloration.

Mimicry

It should be made clear at this point that the immunity from predation which protective resemblance brings is very far from complete. There is good reason for this, as has already been mentioned, but the point to be brought out now is that the survival value of this device, though beyond question, appears to be of a low order when stated quantitatively. It has been calculated for instance that if an animal by resembling its background gains an advantage of one per cent over another that does not, this will still be an advantage worth having.

This consideration applies both to what has been written so far and to what is now to come, namely mimicry. That also is camouflage, since it involves protective resemblance, but of a different kind. It is a matter of resembling, not the background of vegetation and soil but some other animal, and as a subject for discussion and theorizing it has an ancestry in the history of biological science just about as long as protective resemblance generally. It affords equally vivid examples of the working of natural selection. As a device enhancing security, it appears to be confined to the world of insects and spiders, which after all is a very large world.

The principle is simple enough Where true mimicry is concerned, the type that involves apparently deliberate imposture, its basis rests on the fact that some insects are equipped with a device formidable enough to cause predators, such as birds and lizards, to regret having attacked them. This may be either a weapon such as a sting or a bite, or an unpleasant flavour.

Clearly such insects are at an advantage; clearly also a defenceless insect, lacking either of these safeguards, might share in the advantage if it were to imitate the appearance of one that possessed one or the other. This is what has happened in a whole host of well-authenticated instances. There is no need for the resemblance to be exact; a general similarity in colour and shape seems to be enough for predators to learn to avoid both mimic and model. It was the English traveller and naturalist H. W. Bates who first drew the attention of the scientific world to this device, as a result of observations made during the eleven years of his wanderings in the Amazon Basin. He found a clear example in the common South American family of butterflies, the *Heliconidae*. These are large, slow-flying insects, conspicuously coloured black and yellow, capable of exuding a malodorous fluid, and given to collecting in large companies. Among them Bates found a few members of an entirely different family, the *Pieridae*. All the other members of that family have their own wing-shape and colour-scheme, but those that consorted with the *Heliconidae* resembled them quite strikingly in both respects, and possessed no means of defence.

This is a simple example and there are many others. Here, in Britain for instance, there are moths known as clear-wings whose wings are largely devoid of scales and so of colour. This gives them a superficial resemblance to hornets which have formidable stings, and natural selection has induced them to make the most of this resemblance by flying during the daytime as hornets do, instead of at dusk after the usual manner of moths (Plate 12b). Again, comparatively few birds eat ants, and in South America there is a spider which has taken to passing itself off as an ant, which is an outstanding example of mimicry seeing that a spider is not an insect, has eight legs instead of six and a body divided only into head and abdomen instead of into three parts, after the manner of insects. The spider gets over these difficulties by modifying the outline of its body and by spacing two of its pairs of legs close together, so that they begin to look like one pair. Quite apart from these drastic alterations, it mimics also the constant twitching movement typical of ants.

Once more in South America, for it is to equatorial latitudes that we must go to find the most striking examples of mimicry, there is the well-known leaf-carrying ant. They are defoliators of trees and move habitually in imposing processions, each ant carrying on high a fragment of leaf like a banner. Occasionally taking part in these processions, a small defenceless bug may be seen. It resembles an ant in outline, but does more, carries a green banner of its own, which is actually a structural outgrowth of its body.

Mimicry of this simple kind, involving mimic and model, is now known as Batesian mimicry, but though simple in itself it has one rather unexpected result, bringing in one instance at least a considerable degree of complication. The unexpected, though entirely logical result is this: the success of an animal species in general is directly proportionate to its numbers, so that the commoner it is the more successful, but with the mimic in Batesian mimicry this will not do. In relation to its model it is quite essential for the mimic to be scarce, for if it is not the whole object of mimicry will be defeated, and the predator, who has to learn by trial and error which insect is palatable and which is not, will be as liable to pick on the mimics as on the model. Here then is a serious risk for the mimetic species, which may for this reason become confronted with the worst catastrophe that can befall any species, namely extinction. So important is this disproportion in numbers between mimic and model that the genuineness of a supposed mimetic association can be tested by means of it. If the supposed mimic is not quite considerably less common than the model, then any fancied resemblance between them is almost certainly a coincidence.

This risk is so serious to a mimetic species that some of them have perfected a device which goes far towards reducing it. This is by means of what is known as polymorphism, which is the existence of two or more outwardly different forms of the same species, found in about the same numerical proportion and within the same habitat. Now if there are two forms of the same species and each of them mimics a different model, then that species can remain twice as abundant as it could if there were

only one form. Thus, here in Britain, we have a hover-fly, *Volucella bombylans*, of which there are two forms. One, with a black body and a red tail, mimics the red-tailed bumble-bee, *Bombus lapidarius*; while the other, with a yellow-bordered thorax and a white tail, does the same with respect to another bumble-bee, *Bombus lucorum*. The hover-fly is considerably less common than its models. A similar kind of polymorphism, having the same object in view, leads to complications in the case of an African swallow-tail butterfly, *Papilio cenea*. Here there are three forms, but it is only the female whose ranks are thus divided. The male is found in one form only, presumably the ancestral one. Each of the three forms of the female mimics a different model, three distinct species of the genus *Danais*, all of them unpalatable to birds. What follows logically from this, but is nevertheless most remarkable, is that eggs laid by any one of the females hatch out into males and into all three female forms.

In addition to Batesian mimicry there is another kind, quite distinct and involving no apparently deliberate deceit. This is called Mullerian mimicry, after a Brazilian naturalist who explained it not long after Bates expounded his theory. In Mullerian mimicry the relationship between mimic and model is on a different footing. There is no question of association between a mimic that is defenceless and a model in some way armed, no sailing under false colours. The two or more kinds of insect noticeably resembling one another are all in some way distasteful to a predator, and wear a similar uniform because they have found that it pays them to do so. It is in fact a sort of voluntary association, as it were a business arrangement making use of the same kind of advertisement and sharing the proceeds. The association works, the business pays, because a predator is required to learn one lesson only, instead of two or three, with the result that the number of individuals in each species that has to be sacrificed for the predator to learn its lesson is a half or a third what it would be if each displayed a separate advertisement. This could be called the original arrangement, but it is worth realizing that it need not continue quite along those

lines, since it is at least theoretically possible for a Batesian mimic to join a Mullerian association, adopting the uniform of the association as a false advertisement. In this way there might arise a complex amalgamation of the two sorts of mimicry. It is possible, though it has yet to be proved, that here in Britain we have an amalgamation of this kind consisting of the common social wasp, some of the solitary wasps, one or two hover-flies, one or two ichneumons, and the wasp-beetle (Plate 12d), all wearing a conspicuous livery of black and yellow, some as it were honestly, others with intent to deceive.

Conspicuous coloration

It is time to turn now to some of the notable exceptions to the general tendency towards harmony of colour and pattern with background. The subject follows logically from the last, since as we have seen, mimicry involves imitation of the conspicuous appearance of the model. I shall be concerned in the first place with those examples of conspicuous coloration that can be explained within the framework of the theory of protective resemblance, in the second with some that fail to fit in, that seem to many observers to be puzzling anomalies.

In mimicry we have for a start an insect provided with some effective means of defence, which adopts distinctive coloration as an advertisement of unpleasant consequences, so that its sting or malodorous secretion can be brought into play before it is too late. Following upon that comes the defenceless mimic. But there are many instances of insects, as well as a few other animals, with highly conspicuous coloration that have attracted no mimics. They give examples of aposematic or warning coloration, and their effectiveness in advertising unpleasant consequences has been proved by experiments in a number of instances.

Some examples are familiar enough. Most people know the larva of the cinnabar moth with its prominent colour scheme of banded black and yellow. They expose themselves freely, often in large numbers on ragwort. Another larva is that of the magpie

moth, common on gooseberry bushes and equally conspicuous. More familiar than either of these is the seven-spot ladybird beetle. The conspicuous banded or diamond patterning of many poisonous snakes is almost certainly aposematic, as is the rattle of the rattlesnake, and the striking black and white uniform of the skunk, serving as a warning of its intolerable stench. Some creatures, insects for the most part, go further than making themselves stand out boldly from their background and have perfected devices that startle the too inquisitive beholder with some sudden and unexpected display. The eyed hawk-moth, for instance, at rest on the trunk of a tree with forewings covering the hindwings, is an inconspicuous object, an example of protective coloration. If touched, it will at once raise the forewings so as to make a sudden display of the brightly coloured 'eyes' on the hindwings. This has been proved to have a startling effect on a bird, so that it made off. A moth, on the other hand, from whose wings the 'eyes' had been brushed off, was promptly devoured. The grotesque larva of the puss-moth has a way of rearing itself up if disturbed, bringing into view an alarming red mask with black 'eyes', while at the other end of the body the forked tail rises, furnished with whips that lash to and fro.

Up to this point I have discussed the theory of protective resemblance as though it were fully authenticated and universally accepted. Assuming for the moment that this is true, we can explain it on the basis of heritable variations, along the lines of the general theory of evolution, by supposing that natural selection, working on variations that cause the beginnings of resemblance, favours these variations and so sees to it that they are handed on to succeeding generations. In this way general resemblance tends to become intensified, while further refinements even down to minute details, as with the Indian leaf butterfly, will be similarly encouraged. Now it is undoubtedly true that protective resemblance is a fact, supported by far too varied a body of evidence to be brushed aside. In spite of this, it cannot be denied that some of the evidence seems to point the other way, that some animals stand out prominently from

their background, and that these exceptions cannot be explained away by any theory of warning coloration.

Dr Charles Elton in *Animal Ecology* cites the Arctic fox, usually thought of as an admirable example of the tendency with its white coat, so closely approximating to a background of snow This of course is the fox's winter phase. But he goes on to point to the awkward fact that in many parts of the Arctic there is another winter phase among these foxes, the so-called blue which is often nearly black. A black fox living in a snow-covered invironment! How is that to be explained? Natural selection seems to have failed conspicuously. He points out further that the Arctic fox often lives on carrion killed by bears, or on caches of food collected and hidden before the onset of winter. In these instances a white coat seems to have little significance Another and more severe critic of the theory is P. A Buxton, author of *Animal Life in Deserts* Buxton does not deny that many desert animals wear liveries of brown, buff, or grey and so harmonize effectively with their surroundings; but, and this links up in an interesting way with the blue or black Arctic fox, points to a whole host of desert animals that have adopted black as their prevailing colour Black, it appears, crops up widely in the deserts of the world among a great variety of animals, from beetles and grasshoppers to birds such as the raven and some of the wheatears Apart from this he points out that many desert animals that appear to be protectively coloured either hunt or are hunted at night, that others live almost entirely underground, while others again offset the advantage arising from their coloration by refusing to remain still.

These and other facts have caused him to deny that protective coloration can have primary importance for desert animals. It seems to operate in many instances, but this he considers to be of secondary significance, and assumes the existence of some other cause for the coloration of animals. This it is reasonable to suppose, if there is such a thing at all, would operate universally and not in deserts only. What we have here in fact, though Buxton does not enlarge upon it, is a rival theory not wholly

lacking either in adherents or in evidence to favour it. Briefly what it amounts to is that there is an intimate physical and chemical relationship between an animal and its environment, and that it is this that determines the colour, the pattern and perhaps even the form of the animal. As for evidence, it cannot be said to be very impressive, but it appears to be established, for instance, that there is a close connexion between the deposition of melanin or black pigment and light, that animals living habitually in caves are mostly pale and tend to turn black if exposed to the sun. It is true also that conditions of high humidity and high temperature favour the formation of black pigment, while low humidity and high temperature favour yellow and reddish-brown pigments. According to this theory then the colour of animals is caused in the first place by this direct relationship with environment, and it is only when this has first taken place that natural selection comes into play. Its role is therefore secondary, and this secondary process may or may not enhance a partially protective colour scheme previously brought about. It perhaps goes without saying that this theory is rejected by most ecologists. If they are upholders of the orthodox theory of evolution they would be almost certain to reject it, if only because it pushes natural selection off the foreground of the stage.

Dr H.B. Cott, in his magnificent and comprehensive book *Adaptive Coloration in Animals*, has much to say concerning these and other criticisms of the theory that coloration is adaptive. With regard to nocturnal predators for instance, while admitting that with them scent is no doubt of primary importance, he denies that this means that sight plays no part at all, as can be realized by imagining how a blind lion or leopard would fare in its hunting at dusk or on moonlight nights. He makes two further important points about nocturnal creatures, whether predators or prey. In the first place, at night, particularly the often brilliantly lit nights of desert or savanna regions, it is not colour that counts but tone. There are many desert animals that burrow underground during the day, emerging

only at night when their pale colour-scheme would be decidedly protective against the pale background of sand or rock. The other point concerns predators and lays stress on the undoubted fact that the eyes of nocturnal creatures, such as the great cats among mammals and owls among birds, are exquisitely adapted in more ways than one for effective use during conditions of twilight and semi-darkness, during conditions indeed which to us would be almost impenetrably dark.

As for the apparently anomalous black coloration of some desert animals which Buxton uses for his attack on the theory of adaptive coloration, Dr Cott believes that in most cases, ravens and wheatears for instance, failure to resemble their background arises from their normal habits which make resemblance unnecessary. He admits to difficulties where the Arctic fox is concerned, but is convinced that other fur-bearing animals assume no special winter garb because none is needed. In fact with regard to the problem as a whole it seems that Dr Cott, by marshalling a most impressive array of evidence and basing his thesis upon it, has succeeded in vindicating the theory of adaptive coloration completely.

12

POSTSCRIPT

RETROSPECT: The most I can have hoped to do in this book is to outline a complicated system, sketch, imperfectly and selectively, a huge and varied panorama. It was inevitable in trying to present this panorama to divide it into a number of parts and to consider one of these at a time. The limitations of the human mind make this necessary. We find difficulty in giving weight at the same time both to the parts and to the whole. Nevertheless it is important that an attempt in this direction should be made, for only then may we hope to grasp that attribute of fundamental unity which is the very essence of the natural world. Only then can we begin to apprehend the fact that each single phenomenon of nature has no meaning, no existence, except by virtue of its relationship with all the other phenomena; that the beauty of the panorama, its illimitable impressiveness, depends on this realization.

Scientists are inclined to avoid words like beauty: the aesthetic appeal of their subject seems to be one that many of them feel ashamed of. This is unfortunate since the examination of phenomena and the relating of them to other phenomena is their whole concern, and it is just there that the beauty is chiefly to be found. But the business of science is to describe rather than to explain. It is true that scientists are called upon to explain up to a point, but it is the explanation of how a principle operates, not why. The ultimate explanation lies beyond the reach of their inquiries. 'This thing,' they say in effect, 'is as I have described it. There it is. Take it or leave it. Don't ask me why it is so, still less whether any directive purpose lies behind it.' Sir Julian Huxley, writing of evolution, states categorically that any purpose we may think we see in the great cavalcade of life stops short within our own minds, is subjective only, apparent not real. Evolution, he believes and here he voices the opinion of the orthodox school, is a product of blind

forces, with no more directive purpose behind it than behind the fall of a stone; to which the plain man might reply that the fall of a stone is at least an expression of the force of gravity and that this force, even in our post-Einstein age, can be said to have no less a purpose than bringing into existence the earth itself, so that it should become the stage on which the drama of life could be enacted. Sir James Jeans on the other hand, some years ago, took a different view, not of evolution but of the universe as a whole, and put out the suggestion that God is a mathematical physicist. This was perhaps an extreme pronouncement, a making of God in the image of man. Nevertheless it is far more acceptable than Sir Julian's to those who see a purposeful design in the world of nature. There is more to be said in its favour, for it clearly implies the belief that I set out at the beginning of this book and now return to, the belief that is to say that whatever mind designed the great panorama of nature did so in terms apprehensible by the human brain, caused the design to be worked out through the mediumship of natural agencies capable of elucidation by the process of reasoning. What after all is the most marked characteristic distinguishing man from the other animals? Not just the possession of a brain, but the capacity to use that brain for disinterested thinking, for speculating about his origin, about his place in the scheme of things, and about the laws governing that scheme.

With this in mind and embracing the general doctrine of Sir James Jeans, though differing from it in one important particular, let me put forward with becoming diffidence another interpretation. The immense and beautiful panorama of nature can be said to have the attributes of a work of art. A musical metaphor is more applicable perhaps than a pictorial one. A symphony is made up of a very large number of musical notes, these notes are welded into musical phrases, the phrases into themes, the themes into movements. The symphony has unity, and unity is achieved by bringing together these component, distinguishable, and even conflicting parts, in such a way that there is brought about a resolution of opposites, a general harmony out of particular discords. It would be straining the parallel

to compare the four movements of a symphony with the four entities of the natural world, earth, atmosphere, plant-life, and animal-life, particularly since in a symphony the movements succeed one another, are expressed separately, whereas in nature all four play their parts simultaneously and mutually, are woven into a counterpoint far beyond the skill even of a Beethoven. But the suggestion can stand if only because it helps to make clear the incomparable superiority of the cosmic symphony of nature over any known to music, or if you prefer it, of the mind of God over the mind of Beethoven. As for purpose, who can define the purpose of the Eroica Symphony? It was the expression in musical form of an urge felt by its composer. Let us be content with a similar definition of the purpose of the Cosmic Symphony.

PROSPECT · What of the future, both the foreground foreseeable, if dimly, and the background encompassed thickly with shadows? The lover of nature, peering thus darkly, is much inclined to arrive at a most pessimistic conclusion. He loves the incomparable true wildernesses of the earth, those stretches of its surface of which a few even yet remain, where the balance of the four great entities, which is the balance of nature in the true sense, has gone on immemorially and inviolably. He sees them encroached upon year by year, sees these bastions of the natural world falling one by one, and is sickened at the thought of what seems an inevitable process if the destiny of man is to be fulfilled. If the natural scheme of things can be compared, as I have suggested, to a work of art, then he will conclude that man, in seeking to turn it to his advantage, is bent on its destruction. Forgetful of the source from which he springs, remembering only the lamentable tale of man's treatment of the other animals, that protracted atrocity in the name of economic need, our nature-lover may well conclude that there is no room on this earth for both nature and man. He may derive consolation from recent indications of a reaction, remind himself that there are bird-sanctuaries in East Anglia, game reserves in East Africa and the Congo, national parks in North America.

But his consolation will be short-lived, since he knows full well that these sanctuaries are in the long run doomed, is well aware that as the population of the world increases at an ever-accelerating rate, avocets will never be given precedence over food production, nor the splendid game animals of East Africa be preserved to posterity in spite of their tendency to give added opportunities to the tsetse-fly. He will remind himself of what has already been done in the way of the destruction of wildernesses, that activities such as the cutting down of forests, the draining of swamps, the irrigation of deserts, the pollution of rivers with filthy effluents, the pollution even of nature's least violable sanctuary, the sea, with the waste-products of oil-burning ships, are all certain to be extended to an enormous and hastening degree. In his despair at the prospect of a world wholly tamed in the interests of man, he will inform himself bitterly that only one thing is calculated to prevent so bleak a consummation, namely man's destruction of himself by nuclear warfare.

All the same our nature-lover's pessimism is excessive in one all-important respect. Up to a point he is right: beyond that point he is fundamentally wrong, and as a lover of nature he ought to be aware of it. For the truth is that the division of the world of man from the world of nature is a false and exceedingly dangerous division; false because it attempts to divide two things that are indivisible, that are indeed not two but one; dangerous because in trying to bring it about man will render this earth uninhabitable as surely by its human as by its non-human denizens. We are beginning to realize now that ecology is a science of the utmost practical importance, that it is not radioactive strontium that threatens the future of mankind, but neglect of the teachings of ecology. Our nature-lover then is right in supposing that the true wildernesses of the earth as such are in the long run doomed. That is a conclusion to which it seems we must ultimately reconcile ourselves with what fortitude we may. For it is one thing to transform a wilderness into an abode of human beings by working hand in hand with nature, by restricting and guiding her exuberance, by taking part in

and preserving her ageless, cyclical processes, and so bringing into existence a countryside in place of a wilderness. That has already been done long ago and successfully, particularly perhaps in western Europe. Here in Britain true wildernesses remain only in those parts of the country that are uninhabitable, at the two extremes of elevation, a few mountain-tops above the 3,000-foot contour-line and the sea-shore between tide-marks. Everywhere else there are either deserts of brick and mortar or an almost wholly artificial, but still delightful, countryside.

That process, as I say, is one thing, permissible, safe, and calculated to endure, because there the essentials of nature's balance are preserved, and the earth can be induced to bring forth fruit in her own moderation. But recently here at home, and far more in other parts of the world, nature's moderation is grudgingly regarded and men are trying even now to improve upon nature, as though such a thing were possible, to speed up natural processes which operate slowly or not at all, to travel the short road when only the long one will take them to their goal. Deforestation, burning, over-grazing, the cultivation of a single crop over square miles of country, all these things on a big scale, together with others on a smaller scale, such as the grubbing up of hedgerows, repeated drenchings of the land with artificial fertilizers, and the scattering of weed-killers and insecticides, do grievous and in time irreversible violence to the delicate balance of natural processes. The result is to make wildernesses of a wholly different kind, howling and catastrophic wildernesses, the absolute sterility of man-made deserts. We know now, and must studiously pay heed to the knowledge, that it is only through intimate understanding of the web that binds all life on this earth, through so ordering things that man lives in harmony with nature, that disaster can be averted and the survival of humanity assured.

Era	*Period*	*Years ago*	*Animals*
QUATERNARY	Holocene	20,000	Man
	Pleistocene (Ice Age)	1 000,000	Modern mammals
TERTIARY OR CENOZOIC	Pliocene	11,000 000	Mammals
	Miocene	25 000 000	Mammals First apes
	Oligocene	40 000 000	Mammals
	Eocene	60 000,000	Mammals Main radiation of birds Mammals and birds
SECONDARY OR MESOZOIC	Cretaceous	135 000 000	Dinosaurs Early mammals Toothed birds
	Jurassic	180 000 000	Dinosaurs First mammals Toothed birds
	Triassic	225 000 000	Dinosaurs Amphibians
PRIMARY OR PALAEOZOIC	Permian	270 000 000	Am[illegible] Re[illegible]
	Carboniferous	350 000,000	Amphibians First insects First seed plants
	Devonian	400 000 000	Fishes
	Silurian	440 000,000	Fishes Molluscs Trilobites
	Ordovician	500 000 000	First fishes Molluscs Trilobites
	Cambrian	600 000,000	Trilobites
PRE-CAMBRIAN		2 000,000,00	Very few fossils

Figure 8 Ages in the history of the earth

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